IMPACTS OF POPULATION-LEVEL REPRODUCTIVE SUCCESS ON RECRUITMENT DYNAMICS IN LARGEMOUTH BASS (*MICROPTERUS SALMOIDES*)

BY

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DISSERTATION

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ABSTRACT

Understanding the mechanisms that govern recruitment in fish populations is fundamental to informing management decisions that are designed to provide sustainable recreational fisheries. The Largemouth Bass (*Micropterus salmoides*) is a popular and widely exploited sport fish that provides exclusively paternal care to its offspring during the reproductive season each spring. While recreational anglers can negatively impact reproductive success of individuals by capturing nesting males, interrupting parental care, and thus facilitating higher embryonic mortality rates through brood predation, it is unclear whether or not variation in reproductive success across a population is an important driver of recruitment. Density-dependent survival of age-0 Largemouth Bass after parental care ceases may compensate for variation in reproductive success earlier in the first year of life. The chapters of this dissertation present the findings of one study that investigates mechanisms determining brood loss and the concomitant reduction in individual reproductive success during a recreational angling event, and two other studies that examine how reproductive success across a population determines recruit abundance. In Chapter 2, I found that 65% of bass nests in natural lakes experienced brood predation, and that higher brood predator density in the vicinity of the nest was associated with increased probability of brood predation, leading to higher rates of abandonment. Angled male Largemouth Bass were held in a live well for 15 minutes and returned to defend their broods after being released in 30 minutes on average. In addition, the consumption rate of brood predators was higher in nests with higher mating success (i.e., number of embryos), but the number of fry consumed was positively correlated with brood predator densities near the nest prior to angling. The size of the remaining brood determined whether or not the male abandoned its nest, while predator density, parental male quality, and initial brood size had little influence

on abandonment decisions, indicating that even catch-and-release angling of nesting bass can have a negative effect on reproductive success. In Chapter 3, I experimentally induced episodic mortality of 50% of embryos across populations of Largemouth Bass in a series of research ponds, which resulted in a 39% reduction in recruit abundance and a 37% reduction in recruit biomass compared to control ponds. Although higher survival rates in the treatment ponds did appear to partially mitigate recruit losses due to that episodic mortality of embryos, compensatory survival was not great enough to overcome the overall reduction in recruit abundance caused by the treatment. In Chapter 4, I utilized long term fish community assessment data in an information theoretic modeling approach to define which combinations of predictor variables from several stages within the first year of life had the strongest relative influence on fall age-0 Largemouth Bass abundances. It was determined that 1) the presence of Gizzard Shad (*Dorosoma cepedianum*) had a strong negative effect on age-0 Largemouth Bass abundance in the fall; 2) regression models that included juvenile Bluegill (*Lepomis macrochirus*) abundance and turbidity best explained variation in age-0 Largemouth Bass abundance when compared to other models and that both variables were positively correlated with recruit abundance; and 3) density of nesting Largemouth Bass was positively correlated with recruit abundance but was less effective at explaining variation in age-0 Largemouth Bass abundance. While predator-prey interactions during the first summer had clear implications for determining year class strength in Largemouth Bass, reproductive success also played a role in recruitment dynamics of the species.

Overall, these findings demonstrate the importance of reproductive success in recruitment dynamics of Largemouth Bass and that especially in systems with intense angling pressure and high brood predator densities, density dependent growth and survival may not ameliorate early

mortality due to brood predation. Furthermore, these findings show that the relative importance of sources of mortality occurring at various stages of the first year of life have variable impacts on determining recruit abundance, likely due to differences at large spatial and ecological scales.

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So now, the time has come for step two …

Jeffrey A. Stein

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CHAPTER 1: GENERAL INTRODUCTION

Understanding the mechanisms of recruitment in fish populations is fundamental to informing management decisions that are designed to provide sustainable recreational fisheries. To be sustainable, populations require the production of enough recruits to replace the number of adults in the spawning stock that are lost to mortality. Natural mortality at all life stages contributes to the overall mortality rate of a population, but it is the fisheries-related mortality rates of juveniles and adults that are affected by angler capture rates. Angler capture rates, therefore, are most often manipulated through regulatory management actions. Catch-and-release angling can greatly reduce harvest and is promoted as a sustainable, conservation-oriented approach to sustaining recreational fisheries. The goal of management strategies that limit harvest is to protect a large enough number of current or future adults to ensure adequate reproduction and, ultimately, adequate recruitment.

Overfishing has clearly demonstrated negative effects on population sustainability in commercial fisheries. In one notorious example, liberal quotas on the commercial harvest of Atlantic cod (*Gadus morhua*) led to the collapse of a fishery that has since struggled to recover despite implementation of a fishing moratorium designed to protect depleted spawning stocks (Myers et al. 1997). Although cod recruitment indices were stable leading into the collapse, significant reductions in year class strength followed shortly thereafter, demonstrating a linkage between spawning stock biomass and recruitment (Rose et al. 2000). The effect of over-exploitation of the spawning stock was a severe reduction in the production of the next cohort of recruits in the population. That outcome demonstrated that any restriction to reproduction at any phase of the life cycle, whether by reducing the number of spawners or by reducing the reproductive output of those spawners, has the potential to have lasting effects on population

sustainability. Negative effects of angling on population sustainability are not limited to reductions of the spawning stock, but may also extend to disturbance of critical life history processes that ensure the survival of future recruits.

The Largemouth Bass (*Micropterus salmoides*) is a freshwater sport fish (family Centrarchidae) that exhibits male parental care and is distributed throughout North America (Barnhart 1989; Noble 2002). The parental care period in Largemouth Bass lasts up to five weeks (Neves 1975), during which time the parental male is highly aggressive in defense of his brood (Suski and Philipp 2004), and foraging by these males is greatly reduced. The aggressive nature of parental male Largemouth Bass while providing parental care (Ongarato and Snucins 1993) increases their vulnerability to angling (Lindgren and Willis 1990), which likely explains high catch rates associated with Largemouth Bass angling during the parental care period. Although the number of males in a population that spawn in any given year may vary across systems and years, that number was estimated to be about one-third of the mature males in a closed population in northern Wisconsin (Raffetto et al. 1990). If a large proportion of nesting males are successfully angled, that angling may cause consistent disruption of parental care across a population, creating the opportunity for significant predation on embryos and/or larvae during the absence of the brood-guarding male. Even if anglers are practicing catch-and-release, angling of the parental males disrupts brood defense and leaves the young vulnerable to predation (Kubacki et al. 2002; Philipp et al. 1997). If the parental male is harvested, parental care is terminated, resulting in the complete loss of the reproductive output of the angled male. It is not at all clear, however, whether or not the cumulative angling-induced brood losses in individual reproductive success across an entire population are large enough to impact lake-wide recruitment levels for a season.

Even though recruitment dynamics in Largemouth Bass have been studied extensively, no critical recruitment bottleneck has been identified. Research primarily has focused on evaluating fisheries-independent sources of mortality in early life stages, specifically centering on assessments of mortality among juvenile young of the year (YOY) during the first summer or first overwinter period (see Parkos and Wahl 2002). A much smaller number of studies have evaluated mortality during the parental care period and its effect on recruit abundance (Parkos and Wahl 2002). Despite a clear understanding of the negative impacts of angling nesting bass on individual reproductive success (Hanson et al. 2008; Philipp et al. 1997; Siepker 2009; Siepker et al. 2007; Steinhart et al. 2005a; Suski et al. 2003b; Wagner et al. 2006), the role of embryonic mortality in setting year class strength is poorly understood. Given the widespread popularity of angling black bass, to effectively manage this important sport fishery, understanding the role of angling in setting mortality rates at early life stages is critical.

Conceptual Model

To facilitate an evaluation of the relative importance of mortality at various stages of the first year of life, I have constructed a conceptual model of Largemouth Bass early life history (Figure 1.1). This conceptual model is divided into four distinct stages of Largemouth Bass early life history: embryos, swim-up fry, age-0 recruits (pre-winter), and age-1 recruits (post-winter). Survival from each of these stages to the next depends on sources of mortality that are unique to those stages. Abundance of embryos is established through reproduction each spring, and mortality rates during this stage are greatly affected by the quality of parental care. After the parental care phase has ceased, offspring mortality is determined by a variety of mechanisms acting on swim up-fry and age-0 recruits during their first summer of life and during their first

overwinter period. These four stages are milestones in the life cycle of Largemouth Bass at which researchers and managers commonly assess survival, mortality, growth and/or abundance, and the mechanisms that affect those values undoubtedly differ across the four stages. The literature is replete with examples of studies that examine one of these stages of the life cycle and the factors affecting growth and survival within it, in search of a linkage between stage specific mortality and recruit abundance. My conceptual model emphasizes the fact that no single life stage, nor single process within a life stage, is likely responsible for setting year class abundance across all systems.

The focus of this review is to highlight the role that recreational angling of parental fish plays as a direct or indirect source of offspring mortality within the first year of life, with special emphasis on angling during the parental care phase, including an assessment of how the negative effect of angling on individual reproductive success may or may not translate into cumulative effects at the population level. Specifically, the goal of this review is to utilize the conceptual model to highlight specific hypotheses for future research that will evaluate whether angling directly or indirectly alters mortality rates of age-0 bass and, therefore, should be an important consideration in evaluating recruitment dynamics in bass populations.

Parental Care

During the spring when water temperatures approach 14°C, mature male Largemouth Bass move into the shallows and construct nests in the substrate, awaiting the arrival of ripe females looking for mates with which to spawn (Kramer and Smith 1962). Mating success (i.e., the total number of fertilized eggs laid in all bass nests during a spawning season) is the first indicator of recruitment potential for a population in any given year. Factors that affect the

number of spawning adults and the fecundity of the females influence mating success and, therefore, play a role in setting the number of potential recruits in a population at this life stage.

The proportion of mature adults that actually spawn in a given year is variable and may depend on factors such as adult post-winter condition (Ridgway et al. 1991), adult individual size (Ridgway et al. 1991), adult population density, spawning experience in previous years, as well as the availability of spawning habitat (Hoff 1991) and weather conditions during the early spring. Angling may affect the number of spawners in a season in three ways. First, angling (past and current) can shape the abundance and size structure of bass populations (see *Spawning Stock*, below). Second, angling of pre-spawning females can result in smaller and perhaps fewer viable eggs and offspring that have later swim up dates (Ostrand et al. 2004), and this could lead to slower growth and lower offspring survival later in the first stage of life. Although the relationship between stress on females from pre-spawn angling events and the size and hatch time of offspring has been demonstrated (Ostrand et al. 2004), whether or not these impacts have a significant role in recruit mortality is unclear. Third, angling of pre-spawning males can result in physiological stress or even injury that might keep a male from actual spawning activities.

For an individual male bass, the number of eggs that hatch and survive to become independent free-swimming fry determines that male's reproductive success. Once spawning in a population has been completed for a given season, the number of independent free-swimming fry produced by all successful nests represents the total reproductive success for that population. As a result, across a population, the number of potential recruits at the completion of parental care (i.e., the total number of independent free-swimming fry produced) depends upon the number of successful nests and the size of the broods in them. In the black basses, besides defending their broods from potential egg predators male parents maintain optimal conditions for

early embryonic development primarily by using their fins to fan the water above the nest to maintain high oxygen levels near the eggs/larvae and to sweep away sediments that may settle on eggs/larvae developing in the nest. Mortality rates during this stage are highly variable and in some cases have been estimated to be as high as 94% and may be density dependent (Knotek and Orth 1998). After the eggs hatch, parental care predominantly consists of defense against potential brood predators. Fisheries-independent mortality during this phase is largely determined by the male's parental care ability (Brown 1984; Gillooly and Baylis 1999; Goodgame and Miranda 1993; Suski et al. 2002; Wagner et al. 2006). Male bass invest considerable energy into protecting eggs, larvae, and fry from predators during the early stages of life when juveniles are highly vulnerable to predation. Particularly important is the duration of the parental care provided by the males; males that guard the broods the longest have the greatest proportion of the offspring surviving (Parkos and Wahl 2010; Sutter et al. 2012). Those males that are the most effective at providing brood defense would be expected to raise more than the expected number of young to adulthood, while low quality parents or parents whose parental care behaviors have been inhibited in some way would be expected to contribute fewer than expected young to the population. As result, although it has not yet been demonstrated conclusively, widespread disruptions in parental care across entire populations would be expected to reduce the reproductive success for a large number individuals and, therefore, reduce the number of potential recruits entering the next life stage.

Angling of nesting bass increases recruit mortality by removing the parental male and exposing embryos to predation during the parental care phase, even potentially causing abandonment of the brood, which results in a complete reproductive failure. Parkos and Wahl (2010) showed that variation in reproductive success can explain variation in annual recruitment

indices within a population in some Illinois impoundments, although prey density during the first summer was also a significant covariate in that study. Angling nesting bass during the early stages of development reduces the reproductive success of individual males (Philipp et al. 1997) and has negative effects on abundance of age-0 recruits (Ridgway and Shuter 1997), implying that angling may be a driver of recruitment dynamics – at least in certain systems. Angler catch rates, brood predator densities, the time of exposure of the nest to predation while the male is absent, consumption rates of brood predators, and rate of nest abandonment by the parental males are all factors that set the magnitude of angling-induced mortality of broods.

Catch rates of nesting male bass are a function of angler effort, the density of nesting males, and their vulnerability (i.e., aggression) to capture. Because of their increased aggression, their proximity to shore, and in many cases their increased visibility to anglers, angler effort can increase dramatically during the spawning season (Einhouse et al. 2002), resulting in higher catch rates, all while few jurisdictions prohibit angling for or require catch-and-release of nesting bass (Gwinn and Allen 2010; Quinn 2002). Nesting male bass are more aggressive at the early stages of embryonic development (Ridgway 1988) and are more aggressive if they are protecting larger broods (Suski and Philipp 2004), making them more likely to strike a lure and be captured by an angler. This implies that aggressive parental males with larger broods are at higher risk of increased brood mortality (Philipp et al. 1997). Because these males are those males that are most likely to produce larger numbers of surviving offspring through parental care, their increased likelihood of capture may result in even larger negative impacts on recruitment. As the brood approaches independence, male aggression has been shown to ease somewhat (Ridgway 1988), but because these parental males also begin roaming greater distances from their broods as the free-swimming fry begin to disperse (Scott et al. 1997), the probability of their capture by

angling would still be significant. Populations that have been heavily exploited for a number of years may have undergone fisheries-induced evolution, resulting in their becoming less vulnerable to angling (Lindgren and Willis 1990; Philipp et al. 2009), lowering catch rates, which may somewhat mediate negative effects on recruitment, but at the same time negatively impacting their parental care abilities (Sutter et al. 2012).

Aggression in parental male bass, which is an important characteristic for effective nest guarding to ensure offspring survival (Parkos et al. 2011; Sutter et al. 2012), has been shown to be correlated with brood predator density (Cooke et al. 2008; Gravel and Cooke 2009; Steinhart et al. 2005a). Parental males expend more energy on nest defense in systems with high densities of brood predators compared to populations with fewer nest predators (Steinhart et al. 2005b). The removal of a nest-guarding male during the reproductive period exposes his larvae to predators (Philipp et al. 1997; Steinhart et al. 2004; Suski et al. 2003b), and that may have a stronger negative effect on brood survival in systems with higher brood predator density. Populations with abundant brood predators, aggressive males, and even moderate angling effort may be at high risk for significant increases in angling-induced mortality rates during parental care.

How long a brood is exposed to predation is a function of the time it takes an angler to land a fish, how long the angler holds the fish in the boat, and the time after it is released that it takes the fish to recover, return to its nest, and resume active defense of its brood. The fact that parental males take longer to recover from an angling event compared to non-nesting adult males (Cooke et al. 2000; Kieffer et al. 1995; Philipp et al. 1997), indicates that parental males have higher metabolic demands, which is compounded by the fact that they do not actively feed on prey during parental care (Hinch and Collins 1991). Exhaustive exercise, air exposure, repeated

handling, and containment in a live well all elicit a greater stress response and reduced locomotory activity, extending the time it takes a male to recover and return to the nest site (Cooke et al. 2002). In fact, parental males exposed to a simulated angling tournament (i.e., held in a live well for extended periods, released greater distances from nest site) took longer to recover from the angling event than males that were angled and immediately released near their nests (Hanson et al. 2007). During the time it takes a parental male to return to its nest, brood predators are free to enter the nest area and consume eggs or larvae. Little is known, however, about the relationship between predator densities, exposure time, and consumption rates of brood predators. Understanding the real impact of an angling event on embryonic mortality is important for quantifying the negative impacts of angling on reproductive success.

Because nest abandonment represents the most extreme impact of angling on reproductive success, understanding the causes and thresholds of nest abandonment is important for describing the role of angling in shaping recruitment dynamics. Reasons for premature abandonment include physiological stress or even physical injury due to angling as well as decreases in brood size through mortality from predation, fungus, disease, siltation, or other extrinsic influences. After an angling event, a male bass may be less willing or able to defend its brood from predators once it returns to the nest, increasing the likelihood of abandonment (Kieffer et al. 1995; Philipp et al. 1997; Siepker et al. 2006; Suski et al. 2003b). Abandonment rates increase the longer a male is held away from its nest during the angling event (Diana et al. 2012; Hanson et al. 2008; Philipp et al. 1997; Siepker 2009) and have been shown to be related inversely to the size of the brood remaining in the nest (Zuckerman and Suski 2013). Moreover, harvest of the nesting male bass undoubtedly results in complete brood decimation by nest predators (Philipp et al. 1997). Just as parental care theory would predict, older males have

lower abandonment rates (Steinhart et al. 2008), which is likely a result of the tradeoff of continued investment in the current brood and the probability of future reproductive success (Gross 2005; Trivers 1972; Williams 1966).

First Summer

Summer represents a critically important period in the survival and recruitment of age-0 Largemouth Bass and is characterized by 1) fry independence, i.e., the end of parental care by adults, 2) ontogenetic diet shifts that facilitate age-0 fish growth, and 3) a wide range of mortality forces that can substantially influence year class strength through both density-dependent and density-independent processes. The termination of parental care infers that age-0 fish must begin addressing the trade off between meeting the foraging requirements for growth and minimizing predation risk. Size-dependent mortality of age-0 Largemouth Bass is common during summer, with smaller fish typically suffering higher mortality rates than larger individuals due to gape limitations of their predators (Christensen 1996; Hambright 1991). As a result, ontogenetic diet shifts that facilitate rapid growth rates, yet minimize mortality, have been shown to be important for age-0 Largemouth Bass growth and survival during summer; higher mortality occurs for age-0 Largemouth Bass that fail to transition to preying on fish during this period (Deangelis et al. 1984; Timmons et al. 1980; Wicker and Johnson 1987).

Angling plays little or no direct role in determining mortality rates at this stage because sizes normally attained by age-0 bass typically are not large enough to recruit to angling gear used by anglers. Density-dependent survival during the first summer life stage, however, is an important consideration in circumstances when angling of nesting males reduces reproductive success. If fewer recruits survive to independence and density-dependent processes are

determining mortality rates in the first summer, then reductions in recruits during the parental care phase may be ameliorated by increased resource-driven survival of age-0 fish. Several studies have demonstrated density dependent survival of recruits in the first year of life (Allen et al. 2011; Gwinn and Allen 2010) but whether early mortality at the embryonic stage is additive or compensatory in Largemouth Bass has remained largely unexplored. In addition, reductions in offspring numbers without reductions in their brood predator densities may result in just the opposite effect, an even higher rate of predation.

First Winter

Overwinter survival of age-0 recruits has been highlighted as the last crucial step for determining Largemouth Bass year class strength, and there is some evidence that survival during this period is commonly size-dependent (Suski and Ridgway 2009), at least in the northern extremes of the range for largemouth and Smallmouth Bass. Mortality during the winter period has been attributed to two major mechanisms, starvation and predation, although clear separation of these two is difficult when undernourished age-0 fish lose swimming abilities and are faced with the need to take increased risk to find and capture food and with the decreased ability to avoid predators. The strength of those mechanisms, however, is dependent on biological, environmental, and individual fish characteristics and varies greatly across latitude. Overwinter mortality likely becomes more important in shaping year class strength in situations where: 1) prey availability is low, and active foraging increases predation risk, 2) water temperatures impair predator avoidance behaviors by age-0 Largemouth Bass, 3) lengthy winter duration depletes lipid stores to critical lows prior to spring, and 4) habitat complexity provides limited refuge from predators. Because swimming ability and lipid storage are directly associated

with body size of individual age-0 Largemouth Bass (Ludsin and DeVries 1997), body size can be a factor in determining overwinter survival. Angling has little impact on recruit mortality during the winter months because overwintering recruits are unlikely to be vulnerable to hook and line gear.

Dissertation Goals and Objectives

Recognizing the difficulty in conducting a single set of experiments that evaluates all possible factors influencing recruit abundance, Parkos and Wahl (2002) assembled an extensive literature review and ultimately proposed a conceptual model that suggested testing the role of environmental conditions in determining whether embryonic or juvenile mortality rates drive recruitment dynamics. They concluded that size-selective mortality during the first summer is likely the most important driver of Largemouth Bass recruitment, and that episodic mortality of embryos during parental care was a less common driver of recruitment. Contrasting the findings of Parkos and Wahl (2002) that size selective mortality drives recruitment, Fuhr et al. (2002) reported age-0 fall abundance reliably predicted abundance of age-1 recruits with no influence of recruit size on overwinter survival in a series of Illinois lakes. Based on their review of recruitment dynamics among centrarchid species, DeVries et al. (2009) posited that for Largemouth Bass, overwinter survival is the most important bottleneck determining year class strength. The relative importance of episodic mortality of embryos, size-dependent survival during the first summer, and density dependent survival in the first overwinter on recruitment dynamics still remains unclear.

The goal of my dissertation is to investigate the role that angling nesting bass plays in determining episodic mortality of embryos and ultimately recruit abundance, and to evaluate the

relative importance of embryonic survival on recruitment when compared to other early life stages. My dissertation first examines mechanisms affecting embryonic survival within the parental care life stage, followed by a test of how survival during parental care affects recruit abundance into the first summer of life. In addition, I use an information theoretic approach to examine the relative importance of life-stage specific survival in determining recruitment.

In Chapter 2, I used a field-based experiment to evaluate the hypothesis that brood predator density, brood size, and time of nest exposure to predators influence consumption rates. This hypothesis predicts that during an angling event embryonic mortality will be highest when predator densities are high and exposure to brood predators is great. In this study, I calculated instantaneous consumption rates in the field to estimate how rapidly brood predators are able to consume embryos and evaluated how predator density, male parental qualities, and mating success affected how quickly a male returns to his nest. Onset of predation, instantaneous consumption rate, and nest exposure time together determine the overall impact of a catch-and-release angling event on brood loss. Lastly, I evaluated the influence of brood loss, along with predator density, parental qualities, and mating success on the male's decision after the angling event to abandon its nest or to continue guarding it.

In Chapter 3, I tested the hypothesis that angling-induced reductions in embryo abundance during parental care result in lower recruit abundance at the end of the first summer. This hypothesis predicts that within a population, higher rates of embryonic mortality due to angling of nesting male bass will result in fewer recruits at the end of the first summer. Using experimental populations established in research ponds of identical size and shape, I simulated brood predation under controlled conditions (i.e., no natural brood predators present) to specifically measure the effect of brood reduction on recruit production. If catch-and-release

angling results in significant brood reduction across an entire population, and recruitment is reduced as a result, management strategies designed to address recruitment problems would need to incorporate the protection of spawning and nest-guarding bass.

In Chapter 4, I utilize long-term data on Illinois impoundments to develop regression models that incorporate stage-specific factors hypothesized to predict recruit abundance, and then employ an information theoretic approach to test the relative strength of stage-specific regression models. If angling of nesting bass results in episodic mortality of embryos to such a degree that recruit abundance is negatively affected, regression models that incorporate angling catch rates, brood predator densities, and other factors related to the parental care life stage should better explain variation in year class strength among populations when compared to models describing the adult spawning stock or first summer survival.

The three studies in my dissertation address aspects of Largemouth Bass reproduction at three scales. Chapter 2 evaluates how predator prey dynamics determine the rate of consumption of eggs/larvae by brood predators, an important consideration in understanding the overall role of angling nesting bass on reproductive success of individual fish. Chapter 3 evaluates how increased mortality of eggs/larvae during the parental care stage are associated with variation in recruit abundance at the population level. Lastly, Chapter 4 evaluates the importance of mortality during the parental care phase relative to other phases of the Largemouth Bass life cycle. The insights gained by these studies will advance the broad scale understanding of the interplay of mortality rates among various life stages and the overall effect on recruitment dynamics in Largemouth Bass.

CHAPTER 2: QUANTIFYING BROOD PREDATION IN LARGEMOUTH BASS (*MICROPTERUS SALMOIDES*) ASSOCIATED WITH CATCH-AND-RELEASE ANGLING OF NESTING MALES

Abstract

Largemouth Bass (*Micropterus salmoides*) is a highly popular and widely exploited sport fish that provides paternal care to its offspring during the reproductive season each spring. During a catch-and-release angling event, brood predators can enter bass nests and consume embryos, reducing the parental male's reproductive success. While the negative impacts of angling nesting bass have been well documented, factors affecting the rate at which embryos are consumed by nest predators have not been studied at either the individual or population scale. We conducted field observations in nine lakes in southeastern Ontario and southwestern Quebec with abundant Largemouth Bass populations and varying brood predator densities to assess what factors affect how quickly brood predation begins once the male is removed, how quickly a male returns to his nest after release, and which males abandon their nests. Among nests with predation (65% of all nests), predation began sooner after the male was angled in nests that had higher densities of brood predators nearby. The mean return time of a male was 30.0 minutes after being held in a live well for 15 minutes. The mean consumption rate for all nests that experienced predation was 20.9 fry predator^{-1} minute^{-1}, and the rate was higher in nests with higher mating success. The number of fry consumed was positively correlated with brood predator densities near the nest prior to angling, and the size of the remaining brood determined whether or not the male abandoned its nest. Predator density, parental male quality, and mating success were not associated with differences in abandonment decisions.

Introduction

Largemouth Bass (*Micropterus salmoides*) is a highly popular and widely exploited sport fish (Barnhart 1989, Noble 2002) that provides paternal care to its offspring during the reproductive season each spring (Neves 1975). Angling effort targeting black bass is often higher during the spring spawning season relative to the rest of the angling season (Einhouse et al. 2002), and the aggressive nature of parental male black bass while providing parental care (Ongarato & Snucins 1993) increases their vulnerability to angling (Lindgren & Willis 1990). Furthermore, as bass angling tournaments grow in popularity (Kerr & Kamke 2003), anglers are catching more bass and holding them in live-wells to adhere to tournament weigh-in procedures. Whether anglers hold nesting bass in live wells until the end of a tournament day or cull smaller fish and replace them with larger fish throughout the day, tournament-style angling during the spawning season increases nest abandonment rates (Diana et al. 2012). Largemouth Bass held in a live well for 1 hour, for example, take significantly longer to return to their nest than immediately released bass, and in the process they can lose 90% or more of their brood, resulting in a high rate of nest abandonment (Hanson et al. 2007). Whether a male is harvested or released, angling the nest-guarding male provides brood predators the opportunity to enter the nest and consume all or some of the embryos (Kieffer et al. 1995, Steinhart et al. 2004), reducing that male's individual reproductive success (Philipp et al. 1997). When angling of nesting bass is pervasive across an entire spawning population, brood predation can negatively impact recruitment (see Chapter 3). Males that have fewer remaining offspring in their nest after brood predation occurs are more likely to discontinue parental care (Zuckerman and Suski 2013); therefore, a better understanding of how brood consumption rates, predation risk, and time of

nest exposure combine to determine the level of brood loss is needed to design effective management strategies for protecting spawning bass.

While the negative impacts of angling nesting bass have been previously demonstrated (Hanson et al. 2007; Hanson et al. 2008; Philipp et al. 1997; Siepker 2009; Siepker et al. 2007; Steinhart et al. 2005a; Suski et al. 2003b; Wagner et al. 2006), factors affecting the rate at which embryos are consumed by nest predators have not been studied either at the individual or population scale. For example, a lake with a moderate density of Largemouth Bass, but with a low density of brood predators, may not require the same level of protection as a lake with a much higher density of potential brood predators. Although potential brood predators such as Bluegill (*Lepomis macrochirus*), Pumpkinseed (*L. gibbosus*), and Rock Bass (*Ambloplites rupestris*) are common in systems with Largemouth Bass, the impact of predator densities on the likelihood of predation has rarely been quantified (see Gravel and Cooke 2009).

The magnitude of brood loss in an unguarded bass nest is a function of the lag time between removal of the male and the onset of predation, a brood predator's instantaneous consumption rate, the predation intensity (number of brood predators feeding in the bass nest), and the duration of predation. Local densities of brood predators as well as the vigor and aggression with which the male bass defends his nest territory may dictate how quickly brood predators encounter the unguarded nest and their willingness to transgress into the nest territory after the male is removed. Nests with higher densities of predators nearby suffer more intense predation once the male is removed than those with lower densities (Gravel and Cooke 2009), which may shorten the time needed to reduce brood size to a level below the male's nest abandonment threshold. The duration of predation is dependent on the duration of nest exposure (the length of time a male is absent from his nest), which increases as male bass are more

exhaustively exercised during the angling event (Kieffer et al. 1995, Cooke et al. 2002), held for longer periods in a live well (Hanson et al. 2007; Neal and Lopez-Clayton 2001) or released at greater distances from the nest site (Philipp et al. 1997, Siepker et al. 2007). Duration of predation is also determined by the time to onset of predation (the time it takes brood predators to first enter the nest after the male is removed), which has been qualitatively shown to be related to local brood predation risk (Gravel & Cooke 2009). Several studies indirectly related the likelihood of abandonment to nest exposure time (Philipp et al. 1997, Suski et al. 2003b, Hanson et al. 2007), but only a few studies have provided direct evidence that brood loss is an important signal to a returning male bass that influences its decision to continue to defend the remaining brood or abandon the nest entirely (Suski and Philipp 2004; Zuckerman and Suski 2013). No study to date has empirically determined the instantaneous consumption rate of brood predators, nor has the relationship between predation intensity, nest exposure time, and brood loss been evaluated in a single experiment.

This study examines how predator density, male parental qualities (size, vigilance and aggression), and mating success (brood size) influence nest predation dynamics. First, we evaluated the influence of these three factors on the time to onset of predation once the male is removed. Second, we calculated instantaneous consumption rates to estimate how rapidly brood predators are able to consume embryos. Third, we evaluated how predator density, male parental qualities and mating success affected how quickly a male returns to his nest (return time). Onset of predation, instantaneous consumption rate, and nest exposure time together determine the overall impact of a catch-and-release angling event on brood loss. Lastly, we evaluated the influence of brood loss, along with predator density, parental qualities, and mating success on the male's decision after the angling event to abandon its nest or to continue guarding it.

Understanding brood predation dynamics has important implications for developing management strategies designed to protect spawning bass and to maximize reproductive success and recruitment.

Methods

Study Design and Data Collection

This study was conducted in a series of nine lakes within a single ecoregion (Abell et al. 2008) located in southeastern Ontario and southwestern Quebec that were all closed to angling by the public throughout the course of the study. All study lakes contained natural Largemouth Bass populations, but with varying densities of known brood predators (Table 2.1), primarily Bluegill (*Lepomis macrochirus*), Pumpkinseed (*L. gibbosus*), and Rock Bass (*Ambloplites rupestris*). During the 2009 spawning season, snorkelers located 70 Largemouth Bass nests containing fertilized eggs prior to hatching (< 2-4 days old), marked them with a numbered plastic tag, estimated the date of spawn based on development of the embryos (Philipp et al. 1985), and determined mating success by assigning an egg score of 1-5 to each brood. Egg score, an ordinal measure of mating success, can be used to estimate the number of swim-up larvae above a nest 1-2 days after swim-up, and is an indication of future reproductive success (Kubacki et al. In Review). Snorkelers were instructed to assign egg scores based on the diameter of the spread of eggs, the patchiness of the distribution of eggs, and the saturation of eggs (i.e., the extent to which eggs were deposited on top of each other) in each nest (Kubacki et al. In Review). On the rare occasion fresh hook wounds (e.g., bruising and/or epithelial damage on or near head and mouth) were observed on a nesting male bass, that individual was excluded

from the study to avoid introducing bias by including nests in which a brood may have been preyed upon during an angling event prior to the study.

After marking the nest, the snorkeler took a position approximately 3 m from the nest for 1-2 minutes to allow the parental male and nearby brood predators to acclimate to the presence of the swimmer. To determine predator density in the vicinity of the nest, the swimmer recorded the number of brood predators within 2 m of the nest at the beginning and end of a 2 minute observation period (Gravel & Cooke 2009). Predator density was calculated as the maximum number of predators observed during this period. The parental quality of each nesting male was quantified by evaluating nest defense vigilance and aggression. First, nest defense vigilance was quantified by recording categorical behaviors of the parental male during the 2-minute observation period prior to angling. The snorkeler recorded whether the parental male was "off" the nest (i.e., greater than 0.5 m from the nest and not chasing potential brood predators), "on" the nest (i.e., directly above or within 0.5 m of the nest), or "chasing" (i.e., engaged in some anti-predator behavior). For each second the male was "on" the nest that male's vigilance score was increased by one, for each second the male was "chasing", the vigilance score was increased by two, and for each second the male was "off" the nest, the vigilance score was decreased by one. Male vigilance is dependent on predator density to some extent in that males with no predators in the vicinity of the nest will not have the opportunity to "chase" and, as a result, the opportunity to increase their vigilance score by two. Second, to quantify male aggression, a controlled test was used to assess the willingness of each parental male to defend its brood. Each male was presented with a Bluegill model that was manipulated by the researcher to mimic nest predation movements, including having the predator model enter the nest, occupy the area immediately above the nest, and make contact with the nest substrate with the model's mouth. During the 1-

minute aggression test, the snorkeler recorded the number of yawns, rushes, and strikes made at the Bluegill model by the parental male, and these were summed to determine the aggression score for that male (Suski & Philipp 2004).

Once pre-angling assessments of predator density, parental male quality, and mating success were completed, the snorkeler moved away from the nest, and two researchers in a boat approached the nest area and angled the male from the nest. Total length (TL) of the male was recorded in mm, and the male was held in a live well for 15 minutes at which time the male was released in the vicinity of its nest. After each male was captured, the swimmer conducted assessments of the brood remaining in each nest at approximately five-minute intervals. The swimmer recorded predation intensity (by observing the number of brood predators present and actively feeding on the brood) and size of the remaining brood as a percentage of the original brood and the time at which the male returned to its nest after release. One day following the angling and release of the male, a swimmer returned to the nest site to determine whether or not the parental male had terminated parental care behaviors and abandoned the nest and to record a 24-hr post-treatment egg score.

Occurrence and Timing of Brood Predation

Statistical analyses (SPSS v.20.0) included several combinations of predictor variables hypothesized to be associated with parameters characterizing the biological and behavioral response brood predation during an angling event. Prior to analyses, Pearson pairwise correlations were calculated for male total length, male aggression, male vigilance, predator density, initial brood size (i.e., egg score), and predation intensity to identify collinear predictor variables. Due to significant correlations among variables describing qualities of the parental

male (male size, aggression, and vigilance), principle component analysis was used to reduce those three variables into a single component (hereafter, male quality) for use in subsequent analyses.

Logistic regression was used to evaluate how male quality, predator density, and egg score determine whether or not predation occurred for a particular nest. Due to the small number of observations in some lakes, a Chi-Square Exact Test was used separately to evaluate the effect of lake on the occurrence of predation and later on abandonment. Cox proportional hazard regression (Cox 1972) was used to evaluate how male quality, predator density, and egg score predicted the length of time to the onset of predation in nests across lakes. Additionally, lake was used as a categorical indicator Cox proportional hazard regression analyses. For both the logistic regression on occurrence of predation and for the Cox proportional hazard regression for the time to onset of predation, egg score was used as a categorical independent predictor using polynomial contrasts. Polynomial contrasts for each egg score level (1-5) were set equal to the predicted number of swim-up larvae for each egg score (ES) based on the conversion equation below (Kubacki et al. In Review).

$$\#\ Larvae = 1157 * ES^2 - 1038 * ES$$

Although there is variation around Kubacki estimates of swim-up larvae abundance determined by egg score, Kubacki found significant differences among scoring levels for Largemouth Bass with the exception of scores 1 and 2, potentially due to underrepresentation of nests at extremely low end of egg score category 1. Two nests with egg scores of 1, therefore, were excluded from the study, reducing the sample size to 68 nests for all analyses.

Brood Predator Consumption Rate

For each nest, an expectation of swim-up larvae abundance (RS_{exp}) was determined based on initial brood size (i.e., egg score) using the conversion equation above (Kubacki et al. In Review). Periodic assessments quantifying predation were recorded at various intervals across different test nests. To facilitate comparisons among nests, estimates of percent brood remaining and predation intensity were calculated for every 5-minute interval (e.g., at 5 minutes, 10 minutes, 15 minutes, and so on) using straight-line interpolation between adjacent, actually observed values. Estimates of the number of expected swim-up larvae remaining after predation (RS_{obs}) were calculated by multiplying RS_{exp} by the percentage of the brood remaining at the last observation (> 60 minutes) or when the male returned to the nest after being released. For each nest, predation intensity (P) was calculated as the mean number of predators across all observations, standardized to a per-minute rate. Instantaneous consumption rates (CR_t) for each nest were based on interpolated 5-minute estimates and calculated for each 5 minute interval as follows:

$$CR_t = {RS_{t-1} - RS_t} \Big/ {\frac{P_{t-1} + P_t}{2}} \Big/ {5\ min}$$

where RS_t is the expected number of remaining swim-up larvae estimated at time interval *t* and P_t is the predation intensity observed at the time interval. Mean consumption rate ($\overline{CR}$) for each nest was calculated as the mean of all observations of CR_t and a generalized linear model was used to evaluate how fixed factors (lake, initial brood size) and covariates (male quality, predator

density) determine differences in mean consumption rate across nests. Tukey's HSD post-hoc test was used to evaluate differences in mean consumption rates across significant predictors.

Male Return and Abandonment

Cox proportional hazard regression was used to evaluate how lake, predator density, male quality, and initial brood size determined the time elapsed between release of the male and his return to the nest (hereafter "return time") on the day of the angling event (i.e., males that did not return on the angling day were excluded from this analysis). Logistic regression was used to evaluate how male qualities, predator density and change in brood size determined whether males abandoned their nests 24 hours after the angling event.

Results

Male vigilance and aggression were positively correlated ($r = 0.36$; $p < 0.01$), male size was negatively correlated with both aggression ($r = -0.31$; $p = 0.01$) and vigilance ($r = -0.35$; $p < 0.01$), but no other predictor variables were correlated (Table 2.1). Principle components analysis reduced male aggression, vigilance and male size predictors to a single component explaining 55.9% of the variation in the data with a negative component loading for male size (-0.739) and positive loadings for vigilance (0.767) and aggression (0.744).

Predation occurred in 44 of 68 nests observed (65%) and the data indicate that certain lakes had a higher proportion of nests that experienced predation (Chi-square exact test = 14.699; $df = 8$; $p = 0.05$). Across all lakes, predation was more likely to occur in nests belonging to smaller but more aggressive and vigilant males (i.e., larger "male quality" component score), and may have been more likely in nests with higher densities of nest predators nearby (Table 2.2).

Where predation occurred the onset of predation was sooner after the removal of the male in nests with higher brood predator densities, and onset of predation varied across lakes (Table 2.3).

Mean consumption rate ($\overline{CR}$) trended higher in nests with higher initial brood size but post-hoc Tukey HSD test did not identify significant pair-wise differences (Figure 2.1). Likewise, mean consumption rate did not vary by male quality, predation intensity (i.e., mean number of predators in the nest) or across lakes (Table 2.4). Overall mean consumption rate for all nests that experienced predation was 20.9 ± 6.5 fry eaten predator^{-1} minute^{-1}, and the instantaneous consumption rate was generally greatest in the first 15 minutes of exposure (Figure 2.2).

After being held in a live well for 15 minutes, the mean return time of a male was 30.0 minutes (95% CI range = 18.7 – 41.3 minutes), resulting in a total time of absence ranging from 33.7 – 56.3 minutes. Return time varied across lakes, but was not associated with variation in predator density, parental male qualities, or initial brood size (Table 2.5). Across all lakes, 15 of 48 (31%) males with nests that experienced predation abandoned their nests after 24 hours while only 3 of 24 (13%) males with nests that experienced no predation abandoned their nest (Chi-Square = 2.508; df = 1; p = 0.11). The probability of a male bass abandoning its nest after 24 hours did not vary across lakes (Chi-square = 2.083; df = 8; p = 0.09), but males with a higher male quality principle component score (i.e., smaller size, greater vigilance and more aggression) and males that lost fewer offspring due to predation were less likely to abandon their nests (Table 2.6).

Discussion

The density of brood predators in the vicinity of a black bass nest varies across lakes (Gravel and Cooke 2009) and is an important component of the complex behavioral dynamics that structure brood predation dynamics during a catch-and-release angling event. The onset of predation as well as predation intensity were related to the number of predators near the nest site prior to angling, indicating that populations with high densities of brood predators are at risk for more immediate onset of intense brood predation after the male is angled. Once predation begins, nests with higher mating success were associated with faster consumption rates by brood predators. Duration of exposure has been shown to be related to how long and under what handling conditions (e.g., air exposure, live well) the male is held by the angler (Hanson et al. 2007). Consumption rates and duration of exposure combine to determine the magnitude of brood loss, which in the current study was greater for males with higher reproductive potential. Additionally, the current study demonstrated that greater brood losses were related to abandonment rates after the angling event. Returning to the nest, however, does not guarantee survival of the remaining offspring because brood loss incurred during the male's absence is a critical factor that determines whether the male will choose to continue providing parental care or abandon its brood (Zuckerman and Suski 2013).

Duration of exposure to brood predation is a critical component of management strategies aimed at reducing negative effects of catch-and-release angling. For example, black bass caught and held by tournament anglers for later weigh-in or to be culled later in the tournament day are highly likely to have their broods significantly reduced or eliminated before they are released and return to the nest. Anglers immediately releasing captured male nesting black bass and practicing proper handling (Pelletier et al. 2007; Suski et al. 2004) will reduce the window of

opportunity for the onset of brood predation and minimize return times, thus lowering the risk of brood reductions that trigger abandonment. There is substantial evidence that larger males typically have larger broods (Philipp et al. 1997), contribute a larger proportion of recruits to the next year class (Parkos et al. 2011), are more aggressive (Ongarato and Snucins 1993) and, therefore, more vulnerable to capture by anglers (Lindgren and Willis 1990). There is some evidence that reduced reproductive success across a population results in reductions in recruitment (Chapter 3), especially in systems with a combination of high angling pressure and high densities of brood predators. Additional research is needed to investigate under which circumstances the reproductive success of nesting bass is a major factor in recruitment dynamics. Further, widespread reproductive failure of the largest, most aggressive parental males has demonstrated the important role of angling nesting bass as a selective force in fisheries induced evolution of the species (Philipp et al. 2009; Wright and Trippel 2009).

Findings in this study indicated that male size was negatively correlated with aggression and vigilance, contrary to other studies that associated male size with higher aggression and reproductive success (Philipp et al. 1997; Suski and Philipp 2004). These studies, however, did not consider how nest site selection might impact predator densities near the nest, and how predator density may affect short-term aggression behaviors. Higher aggression in larger males may be a factor in the ability of larger males to secure higher quality nest sites that have less exposure to brood predators. Once large, aggressive males secure a high quality nest site with fewer nest predators in its vicinity, aggressive behaviors may diminish slightly, resulting in lower aggression and vigilance scores. Smaller males may have been relegated to lower quality nests sites with higher local predator densities near those nests, causing the smaller males to be more active in nest defense behaviors, resulting in their higher aggression and vigilance scores in

this study. Future studies should evaluate nest site quality relative to exposure to nest predators and the importance of local predator densities on male aggression.

Fisheries managers must balance the goal of providing quality angling opportunities throughout the year with the need to protect spawning bass to ensure successful reproduction in the population. A few jurisdictions implement restrictions on angling nesting black bass during the spawning season (Einhouse et al. 2002; Quinn 1996) in recognition of the potential negative effects of disturbing parental care on offspring survival. Angling restrictions can include complete closure of spring black bass fisheries to restrict angling, immediate catch-and-release only, and a restrictive bag limit (Suski et al. 2002). To balance the need for providing angling opportunities with the need for protecting spawning black bass, managers should evaluate predator densities when considering the need for regulations that restrict angling during the spawn. The effectiveness of implementing immediate catch-and-release only restrictions, for example, will vary (e.g., Kubacki et al. 2002) in large part because the risk of brood predation varies across lakes. Managers could evaluate how typical angler catch rates during the spring spawning season match up with estimates of brood predator abundance across lakes to assess the level of risk associated with angling for nesting bass. In cases where angler catch rates and brood predator densities are high, brood predation is likely to occur quickly and have significant negative impact on brood survival; therefore leaving such a fishery open to catch-and-release angling during the spawning season should be avoided.

CHAPTER 3: EFFECTS OF SIMULATED BROOD PREDATION ON RECRUITMENT DYNAMICS IN LARGEMOUTH BASS (MICROPTERUS SALMOIDES)

Abstract

Angling of nest-guarding male Largemouth Bass (*Micropterus salmoides*) during the parental care phase disrupts brood defense, leaving offspring vulnerable to predation. Unless the angling-induced predation of the offspring during the parental care phase is compensated by increased survival rates later in the first year of life, it may be a critical factor in determining year class strength within a population. The goal of this study was to simulate brood predation in Largemouth Bass and test whether or not reductions in brood caused decreases in recruit abundance, biomass, size and/or condition. Populations of adult bass were established in eight experimental research ponds for each of two years and allowed to spawn. During the spawning season in each year, snorkelers located every nest in each pond, and in treatment ponds each brood was experimentally reduced in size by 50% to simulate predation by brood predators during an angling event. Recruit survival rates and recruit biomass production were not statistically different between treatment and control groups indicating neither density-dependent survival nor growth was detected as a compensation mechanism for brood losses. Survival rates and biomass production, however, did trend higher in treatment ponds indicating that density dependence may have partially mitigated recruit losses due to the simulated brood predation but compensatory survival was not great enough to overcome the overall reduction in recruit abundance caused by the treatment.

Introduction

The Largemouth Bass (*Micropterus salmoides*) is a popular and widely exploited sport fish (Barnhart 1989; Noble 2002) that provides paternal care to its offspring during the reproductive season each spring (Neves 1975). The aggressive nature of male black bass while providing parental care (Ongarato and Snucins 1993) increases their vulnerability to angling (Lindgren and Willis 1990; Suski and Philipp 2004; Wagner et al. 2006). Angling of nest-guarding males disrupts brood defense, leaving offspring exposed to predation (Kubacki et al. 2002; Philipp et al. 1997). Angler pressure on and catch rates of black bass are often higher during the spring spawning season relative to the rest of the angling season (Einhouse et al. 2002), which may cause consistent and widespread disruption of parental care resulting in lower reproductive success (i.e., abundance of free-swimming larvae) across a population.

In taxa where defense against predation is an important component of parental care, the failure of a large number of parents in a local population to adequately care for their young can result in reduced potential for population growth (Lloyd et al. 2005). Removal through angling of the nest-guarding male creates the opportunity for substantial predation on embryos and/or larvae during the absence of that male (Philipp et al. 1997; Steinhart et al. 2005a). If the parental male is harvested, the result is the complete loss of the contribution of that male to the next cohort of recruits (Beeman 1924; Coble 1975; Kelley 1968; Neves 1975; Philipp et al. 1997; Suski et al. 2003b). Anglers practicing catch-and-release, however, may still influence the ability and willingness of the male to continue providing effective parental care and, therefore, affect the number of young surviving to independence. The longer a male is held away from the nest, the longer his brood is exposed to the risk of predation, increasing the likelihood the male will abandon parental care altogether (Philipp et al. 1997; Suski et al. 2002).

Widespread angling-induced brood predation across an entire population may be a critical factor in determining year class strength unless the resultant angling-induced mortality of the offspring during the parental care phase is compensated by increased survival rates later in the first year of life. Although it has been demonstrated that catch-and-release and tournament angling of nesting male bass can lead to complete loss of an entire brood when the parental male abandons the nest (Diana et al. 2012; Philipp et al. 1997; Suski and Philipp 2004), population-level studies examining potential compensatory mortality effects have not yet been reported (Cooke and Schramm 2007). In a review of the literature, Parkos and Wahl (2002) reported that 50% of studies examining recruitment effects at the embryo stage and 30% of studies focusing on the larval stage found significant mortality that critically affected abundance of recruits. Only two studies, however, linked predation of embryos and/or larvae to changes in recruitment (Miller and Kramer 1971; Mullan and Applegate 1968), and only one study (Philipp et al. 1997) directly linked angling of the parental male to increases in nest predation. Parental care imparts positive effects on offspring survival that increase the likelihood that the offspring of an individual will contribute to the next year class of recruits (Parkos et al. 2011). In a recent study of Florida Bass (*M. floridanus*) populations, Allen et al. (2011), demonstrated linkages between reproductive success and recruitment and argued that density dependent survival stabilizes fluctuations in recruitment and presumably ameliorates high mortality rates during parental care. The specific relationship between reproductive success and offspring recruitment might depend on the level of brood predation (Parkos et al. 2011), but clarity on the roles of reproductive success and density dependent survival of offspring in determining recruit abundance has not been achieved.

Understanding how angling nesting male Largemouth Bass impacts recruitment at the population level is important for developing truly effective management strategies for maintaining healthy populations of Largemouth Bass. If catch-and-release angling results in significant brood reduction across an entire population, and recruitment is reduced as a result, management strategies designed to address recruitment problems should consider the protection of spawning and nest-guarding bass. Such strategies may include closed seasons (Kubacki et al. 2002), fish sanctuaries (Suski et al. 2002), habitat modification (Bozek et al. 2002), and/or other regulatory mechanisms (Quinn 2002). The goal of this study was to test whether or not simulated brood predation on nesting Largemouth Bass would result in decreases in recruit abundance, biomass, size and/or condition.

Methods

Study Design

This study was conducted in eight 0.3-acre research ponds located at the Aquatic Research Facility of the Illinois Natural History Survey in Champaign, Illinois. In mid-March of 2007 and 2008, ponds without fish were partially drained to slow early growth of aquatic macrophytes in the littoral zone, thus facilitating behavioral observations during the experiment. Low water was maintained for 2-3 weeks, and then ponds were filled to standard full volume. One week later, ponds were stocked with approximately 11 male and 9 female adult Largemouth Bass (Table 3.1) when water temperatures reached 10°C, allowing bass to acclimate to pond conditions prior to the onset of spawning at 15°C (Ridgway et al. 1989). For each fish, total length (mm) and weight (g) was recorded, scales were collected for age determination, and a PIT tag was injected in the peritoneal cavity for later identification of individuals. The putative

gender of bass was determined by visual inspection of the urogenital opening. Adult males were given a soft dorsal fin clip, and females were given a lower caudal fin clip for gender identification by swimmers during the study. Two individual adult bass (one in each study year) putatively identified as females were actually misidentified males, based on swimmer observations of those two fish with lower caudal clips building nests and defending broods.

This experiment utilized a crossover design where in the first year, ponds were randomly assigned as either a control pond or a treatment pond, and in the second year assignments were reversed (Table 3.1). After ponds were stocked with adult bass, swimmers regularly monitored each pond to determine the onset of spawning. Once spawning activities were observed and males began nest-guarding behaviors, nests were marked with a uniquely numbered nest tag, and guarding males were identified by approximate length and fin clip. Each nest was assigned an egg score on a scale from 1 (low) to 5 (high) to estimate the number of eggs in the nest (i.e., mating success; Kubacki et al. In Review), and stage of egg/larvae development were recorded for each nest (Philipp et al. 1985). Swimmers observed parental care activity and development of each brood every 3-5 days until larvae reached the independent free-swimming stage or parental care activity ceased. A given brood was considered successful only if the male raised the offspring to the independent free-swimming stage. In treatment ponds, a swimmer approached the nest of each male during the egg stage of development and removed 50% of that brood with a turkey baster to simulate brood predation during an angling event. As a procedural control, swimmers also approached nests in control ponds, but none of these broods were devalued.

In mid-August of each year, each pond was drained, and all adults and recruits produced were collected. Because the measurement of recruit abundance was conducted in August, any variation in overwinter survival among ponds was eliminated. Recruits from each pond were

counted and weighed in bulk with the exception of a random sub-sample of at least 200 individuals. When recruits were larger than 2 standard deviations than the mean recruit total length, they were labeled as cannibals and analyzed as a covariate as described below.

Analysis

Egg scores for reproductively successful nests were used to determine the number of free-swimming larvae expected to be produced from each nest using the Kubacki (In Review), conversion equation (see page 22). For treatment pond data, the calculated estimate for total number of free-swimming larvae was reduced by 50% to reflect the removal treatment. Only the estimated numbers of offspring from successful males were included in subsequent analyses of recruit production. At the pond draining, recruit abundance was determined by direct count, and recruit biomass was determined by summing the individual weights of the subsampled recruits with bulk weight measurements of the remaining recruits.

For each treatment and control pond, a recruit survival rate was calculated as the number of non-cannibal recruits recovered divided by estimate of free-swimming larvae for that pond. Similarly, the recruit biomass produced was calculated as the total biomass of recruits recovered divided by the estimate of free-swimming larvae for that pond. This analytical approach accounts for natural variation in female fecundity and nesting success among ponds. Because the recruit survival rate and recruit biomass production are proportional data, they were arcsine square root transformed prior to analysis. Linear mixed models (MIXED procedure in SPSS 20.0) with treatment group, pond, and year included as fixed effects and a random effect accounting for the influence of cannibals was used to evaluate the response of four measurements of the recruit population to the treatment. Models predicting recruit survival rate,

biomass production, mean total length, and mean Fulton's condition factor K were the dependent variables in each model and a corresponding random effect of cannibals (i.e., cannibal survival rate, cannibal biomass production, cannibal mean total length, and cannibal Fulton's condition factor) was included in the model. If recruit survival and growth was density dependent in a compensatory response to simulated brood predation, recruits from treatment ponds should have significantly higher survival and growth rates, resulting in greater total length and higher condition factors.

Results

Adult Largemouth Bass were randomly distributed among ponds and ranged from 3+ to 11+ years old based on aging of scales. Based on two-way ANOVA, there was no significant difference in TL either among adult males ($F= 0.325$; $df = 15,161$; $p = 0.99$) or among adult females ($F = 0.411$, $df = 15,128$; $p = 0.97$) across ponds and years (Table 3.1). In addition, although some natural abandonment occurred in both groups of ponds in both years, nest abandonment rates were similar in control ponds (12.5%) and treatment ponds (8.5%) across years (Fisher's Exact Test; $p = 0.57$). Similar rates of natural abandonment indicate that brood devaluation did not trigger widespread nest abandonment in treatment ponds. In the second year, two individual males made a second attempt to nest late in the spawning season, but both were unsuccessful, accounting for the 13 nests in a pond stocked with only 11 males. Finally, the level of reproductive success was similar between the treatment and control ponds across years; i.e., there was no significant difference between control and treatment ponds in the mating success of the males, and therefore, in the estimates of free-swimming larvae of successful nests ($F = 2.099$; $df = 1,14$; $p = 0.17$). Abundance of large recruits that were cannibals averaged less

than 1% of the recruits across all ponds and the proportion of cannibal biomass averaged 7.3% across all ponds. The proportion of cannibals was not correlated with recruit survival rate ($r = -0.12$, $p = 0.66$), and the proportion of cannibal biomass was not correlated with recruit biomass production ($r = -0.06$, $p = 0.83$).

The linear mixed model of recruit survival rate showed no significant difference between control and treatment ponds ($F = 3.639$; $df = 1,5.063$; $p = 0.11$; Table 3.2) with no significant pond ($F = 1.120$; $df = 7,5.111$; $p = 0.47$) or year ($F = 2.206$; $df = 1,5.762$; $p = 0.19$) fixed effects and no significant random effect of cannibal abundance (Wald $Z = 0.514$; $p = 0.67$). Brood reductions had a small effect on recruit survival (Cohen's $d = 0.21$), which did trend higher in treatment ponds (Figure 3.1). There was no significant difference in recruit biomass production between control and treatment ponds ($F = 3.591$; $df = 1,6$; $p = 0.11$) with no significant pond ($F = 1.808$; $df = 7,6$; $p = 0.24$) or year ($F = 4.312$; $df = 1,6$; $p = 0.08$) fixed effects and no significant random effect of cannibal biomass (Wald $Z = 0.514$; $p = 0.67$). Brood reductions had a moderate to large effect on recruit biomass (Cohen's $d = 0.71$), which trended higher in treatment ponds (Figure 3.2). Mean total length was similar between treatment and control ponds for non cannibal ($F = 0.002$; $df = 1,14$; $p = 0.96$) and cannibal recruits ($F = 0.199$; $df = 1,12$; $p = 0.66$). The mean weight of individual recruits from treatment ponds was 1.8 g (SE = 0.2), which was not statistically different ($F = 0.021$; $df = 1,14$; $p = 0.89$) from the mean weight of non-cannibal recruits from control ponds (1.9 g; SE = 0.3). Furthermore, condition factor among recruits was consistent and showed no significant differences between treatment ponds and control ponds across years ($F = 0.014$; $df = 1,6$; $p = 0.907$).

Discussion

Largemouth Bass commonly coexist in diverse fish assemblages that include a variety of potential brood predators. In an angling event, embryos are left vulnerable to predation during the time it takes an angler to land the fish, remove the hook, and perhaps weigh, measure, and photograph it prior to release, as well as for the time it takes the male to return to its nest (Kieffer et al. 1995; Philipp et al. 1997). As competitive bass angling tournaments held during the spring spawning season grow in popularity (Kerr and Kamke 2003), a larger number of nesting bass are likely to be angled and held in live wells for long periods prior to the weigh-in and eventual release, thereby greatly increasing the amount of time it takes a male to return to his nest from the point of release (Diana et al. 2012; Hanson et al. 2007). Longer absences from the nest site are associated with a higher incidence and intensity of brood predation, which will reduce the number of offspring produced from that nest that reach independence at the end of parental care. (Philipp et al. 1997). Furthermore, as the amount of brood predation increases, the likelihood of nest abandonment (with the concomitant loss of the entire brood) increases as well (Philipp et al. 1997).

Although some form of recruitment compensation has been suggested as a mitigating influence to any possible brood predation across populations there is no evidence for or against the existence of compensatory survival and growth during the first year of life. On the other hand, there are no published studies indicating whether or not angling-induced brood loss on a population-wide scale is ever large enough to produce a population-level response in recruit abundance, biomass, size, and/or condition. If some form of density-dependent survival and growth, either during parental care or later into the first year of life, is compensating for the elevated rates of embryonic mortality caused by angling-induced brood predation, then recruit

abundance, biomass, size, and condition should be similar in systems with and without substantial angling-induced brood predation. Furthermore, for populations in which density-dependent survival compensates for angling induced brood losses, post-brood loss survival rates should be higher than populations in which there are no angling-induced brood losses. In our study, if treatment ponds had fewer recruits competing for limited food resources, then growth rates would be expected to be higher than in control ponds.

In this study, although recruit survival rates in treatment ponds tended to be higher indicating some compensatory survival, differences were not significant indicating that brood losses were partially compensated via low levels of density-dependent survival. Because the recruits in treatment and control ponds were similar in TL, weight, and condition, I conclude that the recruits in the treatment ponds did not experience density-dependent increases in growth in response to brood losses. Despite the low statistical power of this study, there was a small effect size in recruit survival rates and a large effect size on biomass production between groups, supporting the conclusion that brood predation has important biological significance in determining recruit abundance, but may not have as strong effect on growth rates.

Abiotic factors such as rapid changes in water level (Kohler et al. 1993; Miranda et al. 1984) or water temperature (Landsman et al. 2011) are important sources of density independent episodic mortality at the embryonic and larval stages of development (see Parkos and Wahl 2002). Brood predation during an angling event likewise results in episodic mortality when two important conditions are met. First, brood predator densities must be high enough relative to the density of bass nests to ensure adequate encounter rates between brood predators and bass nests. Second, angling pressure must be high enough to impact a large proportion of nests in the bass population. In systems where brood predator densities and angling pressure are sufficiently high,

brood predation may be an important source of episodic mortality at embryonic and larval stages of development.

There is growing evidence that the number of reproductively successful nests in a Largemouth Bass population is an important factor in determining recruit abundance (Parkos et al. 2011; Philipp et al. 1997; Pine et al. 2000; Siepker et al. 2006). Negative impacts of episodic mortality (e.g., brood predation) during early stages of development is likely much more acute among populations that have limited windows of time to spawn and hence to re-nest following nest abandonment. Likewise in systems where angling pressure is intensified during the spawning season and brood predator densities are high, recruitment is more likely to be negatively impacted by angling-induced brood predation. Understanding the relationship between annual spawner density, angling pressure, and predator density can assist managers in assessing angling-related risks to successful recruitment. Where angling pressure during the spawning season and brood predator densities are high, managers should consider strategies that reduce or limit mortality of embryos/larvae, such as mandatory catch-and-release, spawning sanctuaries, or closed seasons. In addition, during the spawning season anglers should be encouraged to release all bass immediately in an effort to avoid holding nesting males away from their nests for any length of time, such as during a typical weigh-in tournament (Siepker 2009). Finally, limiting embryonic mortality due to angling induced brood predation can be part of a conservative approach to managing highly exploited Largemouth Bass populations.

CHAPTER 4: A MODEL SELECTION APPROACH TO ASSESSING COMPLEX RECRUITMENT DYNAMICS IN LARGEMOUTH BASS

Abstract

Although Largemouth Bass (*Micropterus salmoides*) recruitment dynamics have been extensively studied, no single critical life stage that sets year class strength has been identified. Various studies have demonstrated that predator prey dynamics during the first summer of life, overwinter survival, and abiotic factors can all be important determinants of recruit abundance. There is also strong evidence that reproductive success may play a key role in recruitment dynamics, but no evidence has been offered to show that variation in reproductive success among individual will in population level effects on recruitment. The goal of this study was to determine the relative importance in determining recruit abundance of variables describing physical habitat, parental stock, reproductive success and predator prey dynamics in the first summer of life using over 20 years of data from multiple reservoirs in Illinois. By evaluating candidate models using an information theoretic approach, it was determined that 1) the presence of Gizzard Shad (*Dorosoma cepedianum*) had a strong negative effect on age-0 Largemouth Bass abundance in the fall; 2) regression models that included juvenile Bluegill (*Lepomis macrochirus*) abundance and turbidity best explained variation in age-0 Largemouth Bass abundance when compared to other models and showed that both variables were positively correlated with recruit abundance; and 3) although the regression model that included density of nesting Largemouth Bass showed a positive relationship with recruit abundance that model was less effective at explaining variation in age-0 Largemouth Bass abundance compared to other models. Predator-prey interactions during the first summer have clear implications for

determining year class strength in Largemouth Bass, parental care also plays a role in recruitment dynamics of the species. Studies to explore further how variation in reproductive success created by angling nesting bass impacts recruit abundance is warranted, as are studies that investigate variation in recruitment dynamics across latitudinal and trophic gradients.

Introduction

Recruitment dynamics in Largemouth Bass (*Micropterus salmoides*) have been extensively studied, resulting in a variety of hypotheses proposed to explain recruit abundance for this important sport fish (see Parkos and Wahl 2002). Those hypotheses have focused primarily on mechanisms operating after the termination of parental care, through the completion of the first year of life (see Ludsin and DeVries 1997). Gizzard Shad can have a strong influence on prey availability through competitive interactions with Bluegill (Welker et al. 1994) and likely play an important role in Largemouth Bass recruitment dynamics. In age-0 bass, for example, early ontogenetic diet shifts from feeding on invertebrates to piscivory have been shown to increase first-year growth rates, leading to increased overwinter survival (Olson 1996). Recruits that make early season shifts to piscivory are better able to exploit available energetically valuable prey resources like Bluegill (*Lepomis macrochirus*) or Gizzard Shad (*Dorosoma cepedianum*) larvae (Garvey et al. 2000), resulting in larger recruits prior to their first winter (Ludsin and DeVries 1997). Larger recruits are thought to have higher overwinter survival due to the relationship between body size, energy stores, and vulnerability to predation (Garvey et al. 1998). Growth rates during the first year of life have been shown to be density dependent in many systems (Garvey et al. 2000; Trebitz 1991), lending support to the hypothesis that recruit survival may be density dependent as well (Allen et al. 2011). Although there has

been little evidence to indicate that adult bass abundance is a reliable predictor of recruit abundance (Parkos and Wahl 2002; Post et al. 1998), there is significant variation within and among populations in the proportion of mature adults to spawn each year (Post et al. 1998). In addition, there is significant variation in the percentage of adults that are successful in producing surviving offspring each year, suggesting that reproductive success of spawning adults within a population may still play an important role in setting year-class strength (Philipp et al. 1997). While a many Largemouth Bass recruitment studies have focused on the first summer of life, little attention has been given to the parental care period when spawning adults protect their offspring during the earliest stages of development.

Largemouth Bass provide parental care to increase survival rates of embryos and to increase reproductive success and individual parental fitness (Gross and Sargent 1985). The Largemouth Bass is a highly popular and widely exploited sport fish (Barnhart 1989; Noble 2002) that has generated a considerable body of research demonstrating how recreational angling of nesting Largemouth Bass can negatively impact individual reproductive success and fitness (Philipp et al. 1997; Steinhart et al. 2005a; Suski et al. 2002; Wagner et al. 2006). Nest abandonment and, therefore, reproductive failure of individual male bass, appear to be triggered by a combination of physiological stress from the angling event (Hanson et al. 2007; Siepker 2009; Suski et al. 2003a) and brood predation during the male's absence of the male (Suski et al. 2003b; Zuckerman and Suski 2013). Reductions in the size of a brood are known to trigger nest abandonment, thereby eliminating any contribution of recruits to the year class by the angled male (Suski et al. 2003b; Zuckerman and Suski 2013). Even if a nest is not abandoned, it is exposed to potential brood predation, and widespread brood reductions across large numbers of nests in a population may reduce the number of recruits produced (Chapter 3). Prey fish

abundance and the abundance of larval Largemouth Bass shortly after the termination of parental care have been linked to variation in recruitment (Parkos and Wahl 2010), but it is still unclear how reproductive success across a population may be associated with variation in recruitment. Although the effects of this increased embryonic mortality on population level recruitment dynamics are not fully understood, the value of protecting spawning bass is evidenced by the use of closed seasons in some management jurisdictions (Quinn 2002) and fishing sanctuaries (Suski et al. 2002). It has been suggested, however, that fishing closures may only be effective in low productivity systems with high densities of adult bass (Gwinn and Allen 2010).

Given the widespread popularity of angling black bass, the importance of reproductive success needs to be evaluated along with recruitment mechanisms that operate in other life stages before the impact of angling on offspring mortality rates during parental care is fully understood (see Ludsin and DeVries 1997). It is likely, however, that no single biotic or abiotic process sets year class strength across all Largemouth Bass populations, and yet, studies that simultaneously evaluate the interaction of multiple factors during several life stages are still lacking. A large proportion of hypotheses explaining recruitment dynamics in Largemouth Bass neglect to consider the importance of embryonic survival rates and the role of parental care. The lack of more holistic studies of recruitment is not surprising given the complexity of recruitment, as well as the wide range of latitudes and environments in which Largemouth Bass are distributed. One potentially effective approach in assessing recruitment processes across multiple life stages is to utilize long-term fisheries data to generate predictive models representing various known and hypothesized recruitment mechanisms. Those predictive models can then be evaluated against each other using an information theoretic approach to identify the best competing models (Burnham and Anderson 2002). This approach can serve as a proxy for logistically and

financially challenging experimental methods of simultaneously evaluating several recruitment processes *in situ*.

The objective of this study was to evaluate the relative importance of the physical habitat, parental stock, reproductive success, and first summer growth and survival on recruitment of Largemouth Bass across a wide spatio-temporal scale. Combinations of multiple regression models, including all of these potential relevant inputs, were assessed in an information theoretic modeling approach to determine those models that best described variation in Largemouth Bass recruitment across broad temporal and spatial scales.

Methods

Data Sources

The physical habitat parameters used in this study were generated from previous work conducted by Illinois Natural History Survey personnel (Austen et al. 1993), while fisheries independent data and creel survey data were obtained from the Fisheries Analysis System (FAS) of the Illinois Department of Natural Resources Division of Fisheries (Bayley and Austen 1987). From these two data sources (creel surveys and electrofishing samples), data were screened to identify reservoirs/years for which fall AC boat electrofishing data existed for two consecutive years, and for which a creel survey had been conducted in the second of those two consecutive years. Standardized electrofishing samples consisted of runs at one or more near shore stations in each reservoir, with each run lasting 20 – 60 min. When multiple sampling runs were conducted on a single reservoir within a fall sampling period, sampling data was pooled across runs and stations. A set of 74 population assessments (1987-2009) across 32 reservoirs (size range of 18 – 750 surface acres) was selected for inclusion in this study (Figure 4.1), and 41

population assessments included Gizzard Shad in the samples. Selected reservoirs were characteristic of Midwestern systems that support sport fish communities dominated by Largemouth Bass as top predator.

Parameters describing the parental stock and brood predator density were sampled by AC boat electrofishing samples in year one, the year prior to a creel survey. Using data from year two, estimates of reproductive success were generated by gathering angler catch data from over 300 stratified random creel surveys (Bayley et al. 1990) conducted on impoundments throughout Illinois from 1987 to 2009. Fall boat electrofishing samples from the same year as a creel survey were selected to generate parameters describing first summer predator-prey mechanisms as well as the response variable, age-0 Largemouth Bass abundance. These data were used to generate response and predictor variables for regression models describing factors influencing Largemouth Bass recruitment.

Physical Habitat

For each impoundment included in the study, surface area (acres), maximum depth (m), mean depth (m), inshore mean depth (m) and shoreline length (km) were generated to define the physical features of the reservoir. Surface area, maximum depth, mean depth, and shoreline length were indicators of overall lake size and bathymetry. Inshore mean depth (m) was estimated as the ratio of littoral zone volume (m^3) and littoral zone surface area (m^2) (Austen et al. 1993), and was used as a measure of potential Largemouth Bass spawning area.

Parental Stock

For each reservoir, data collected during the fall electrofishing of the first of two consecutive sampling years were used to calculate estimates describing parental stock. Individual Largemouth Bass 350 mm total length or larger collected during fall electrofishing were considered adults (Carlander 1977). For each sample, relative adult abundance (fish hr^{-1}), relative adult biomass (kg hr^{-1}), and relative weight (W_r) were used to characterize the parental stock, whereas proportional stock density (PSD) was used to characterize population size structure.

Reproductive Success

Daily surface water temperature data, recorded during creel surveys, were used to estimate the start of the Largemouth Bass spawning season was estimated to be the date at which water temperature reached or exceeded 14 °C for at least three consecutive days (Ridgway et al. 1989). The end of the parental care period season was conservatively estimated to be 35 days after the estimated start date (Kubacki et al. 2002). Using creel survey data, angler catch during the parental care period was used to estimate the density of nesting bass (fish per km shoreline) assuming that anglers targeting Largemouth Bass were targeting near shore areas during the spawning period. We assumed that the length of shoreline was proportional to the total amount of spawning habitat in each reservoir. To calculate the total number of nesting Largemouth Bass caught by anglers during the 35-day spawning period, angler catch totals of Largemouth Bass from the creel survey were summed across all angler interviews conducted during the estimated spawning season. The release ratio of adult bass was calculated as the proportion of all Largemouth Bass caught by anglers that were released (and not harvested). Estimates of the

number of nesting bass angled were then standardized by the kilometers of shoreline of each reservoir to facilitate comparisons among impoundments in regression analyses. Nine centrarchid species, and nine of their various hybrid combinations (*Lepomis macrochirus*, *L. gulosus*, *L. cyanellus*, *L. microlophus*, *L. megalotis*, *L. humilis*, *Pomoxis nigromaculatus*, *P. annularis*, *Ambloplites rupestris*) were enumerated to calculate relative abundance (fish hr^{-1}) of potential brood predators in each impoundment. Brood predator abundance were considered to represent the risk of nest predation during an angling event (Gravel and Cooke 2009).

First Summer Growth and Survival, and Recruitment

Turbidity was estimated as the average of all secchi depths recorded by creel clerks throughout the March to October survey period each year. Daily high and low air temperatures, recorded at weather stations (http://www.ncdc.noaa.gov/cdo-web/) near each impoundment, were used to calculate growing degree-days (14 °C base) for the entire creel survey period each year (Philipp et al. 1985). The mean percent coverage of submerged aquatic macrophytes was visually estimated during electrofishing runs and was used as an indication of lake productivity and available cover habitat for juvenile fish. Boat electrofishing data in the fall of the second year were used to quantify the abundance of juvenile Bluegill (fish hr^{-1}), as well as the abundance.

Largemouth Bass less than 150 mm total length captured during fall electrofishing were considered age-0 recruits based on published standards of back calculated size-at-age values for North American Largemouth Bass (Jackson et al. 2008), mean size-at-age values for Illinois Largemouth Bass (Carlander 1977), and length frequency histograms of all 74 reservoir surveys. In two samples (Beaver Dam Lake, 1993 and Sam Parr Lake, 1987), length frequency histograms indicated 170 mm and 180 mm thresholds (respectively) were warranted.

Statistical Analyses

Recruit abundance exhibited a Poisson distribution this variable was log transformed prior to regression analyses. Based on residual plots, juvenile Bluegill abundance and secchi depth demonstrated heteroscedasticity, and, therefore, were log transformed prior to regression analyses. Two proportional variables (release ratio and percent weed cover) were arcsine square root transformed prior to regression analyses. Finally, multicollinearity diagnostics were used, along with the correlation matrix of all predictors, to identify groups of variables that co-varied to eliminate duplicative variables from the analysis.

Four candidate multiple regression models predicting fall age-0 recruit abundance were generated using the general linear model (GLM) procedure in SPSS (IBM 2011). The habitat model included maximum depth and mean inshore depth and the parental stock model included abundance, biomass, proportional stock density, and relative weight of adults. The reproductive success model included the density of nesters, the abundance of brood predators and the proportion of angled bass that were released by anglers. The summer growth and survival model included juvenile Bluegill abundance, secchi depth, growing degree-days, percent weed cover and the presence of Gizzard Shad. Akaike's Information Criterion (AIC_c) model selection procedures (Akaike 1992) were used to determine the best fitting model or combination of models, including a global model. Models with ΔAICc values ≤ 2.0 were considered strongly supported, while models with ΔAICc values > 2.0 and < 5.0 were considered moderately supported.

Results

The multiple linear regression model that best predicted age-0 Largemouth Bass recruit abundance indicated that impoundments that were less turbid and contained no Gizzard Shad had higher abundances of Largemouth Bass recruits (Table 4.1). While the presence or absence of Gizzard Shad was a strong predictor of age-0 Largemouth Bass, the density of gizzard in an impoundment did not influence abundance of age-0 Largemouth Bass in the fall ($F = 0.380$; $df = 1,30$; $p = 0.542$). Although additional models that included secchi depth, juvenile Bluegill abundance, and nester density were also among the most competitive for predicting age-0 recruit abundance during fall electrofishing (Table 4.1), in each model, regression coefficient estimates for variables other than Gizzard Shad presence were not significant. Recruit abundance in reservoirs without Gizzard Shad ($n = 33$) had a high coefficient of variation ($CV = 1.94$) compared to impoundments with Gizzard Shad ($CV = 0.74$); therefore, information theoretic modeling was repeated only for impoundments with Gizzard Shad. Shoreline length and surface area were strongly multi-collinear with several other variables, they were both excluded from further analyses.

Among the 41 impoundments containing Gizzard Shad, the multiple regression model that included juvenile Bluegill abundance and secchi depth best explained variation in recruitment indices, and the second best model showed moderate support for including nester density (i.e., reproductive success) along with juvenile Bluegill abundance and secchi depth (Table 4.2). In this three parameter model, coefficient estimates and partial regression plots showed positive relationships with juvenile Bluegill abundance and secchi depth, indicating that less turbid impoundments with higher densities of juvenile Bluegill had higher Largemouth Bass recruit abundance in the fall (Figure 4.2A-B). Although the partial regression plot for nester

density (i.e., reproductive success) was not significant in the multiple regression model (Figure 4.2C), the univariate regression of nester density and recruit abundance showed a significant positive relationship between nester density and fall abundance of age-0 bass ($r^2 = 0.48$; $F = 11.385$, $df = 1, 39$; $p = 0.002$). Results of information theoretic modeling, therefore, indicate that although variables not related to reproductive success were the most effective predictors of fall age-0 recruit abundance among the models included in this study, reproductive success also provides some explanatory power regarding variation in recruitment dynamics among Largemouth Bass populations.

Across the physical habitat variables examined, impoundments with deeper inshore areas and greater maximum depths were associated with higher age-0 recruit abundance in year two fall electrofishing samples (Table 4.3). Adult condition (W_r) quantified during fall electrofishing (i.e., leading into the winter before spawning) was the only variable characterizing the parental stock that was predictive of fall age-0 recruit abundance, and was negatively correlated with recruit abundance (Table 4.3). Univariate models of adult biomass, adult abundance and proportional stock density (PSD) of the Largemouth Bass population in the fall prior to the spawning season were not significant predictors of fall age-0 recruit abundance (Table 4.3).

Among the variables characterizing reproductive success, impoundments with higher densities of nesting Largemouth Bass had higher abundances of fall age-0 recruits, but densities of potential brood predators ($\beta = 2.405 \pm 1.278$ SE; $p = 0.07$) and the angling release ratio ($\beta = 0.249 \pm 0.138$ SE; $p = 0.07$) had little influence in predicting fall age-0 recruit abundance (Table 4.3). Higher densities of juvenile Bluegill, greater secchi depths, and the absence of Gizzard Shad were each positive indicators of fall age-0 recruit abundance, while weed cover and growing degree days showed no relationship with fall age-0 recruit abundance (Table 4.3).

Abundance of Largemouth Bass recruits was significantly lower in impoundments with Gizzard Shad (Figure 4.3A). Impoundments with Gizzard Shad also had lower densities of juvenile Bluegill (Figure 4.3B) and lower mean secchi depths (Figure 4.3C).

Mean fall age-0 recruit abundance was 0.62 recruits hr^{-1} electrofishing effort (SE = 0.07) and varied over 60-fold across all samples included in the analysis (range = 0.04 – 2.48). Based on an ANOVA, mean total length of Largemouth Bass recruits was 110 mm in impoundments without Gizzard Shad and 111 mm in those impoundments with Gizzard Shad ($F = 0.021$; df = 1,72; $p = 0.886$)

Discussion

The presence of Gizzard Shad was strongly associated with age-0 Largemouth Bass abundances, indicating the importance of complex fish community interactions in determining recruitment relative to other variables such as physical habitat and reproductive success. Gizzard Shad larvae typically hatch early and grow rapidly, escaping predation by juvenile Largemouth Bass (Hambright et al. 1991), outcompeting Bluegill juveniles, and depleting zooplankton prey (Dettmers and Stein 1996; Welker et al. 1994). The negative effect of Gizzard Shad on zooplankton and juvenile Bluegill affects prey availability for juvenile bass, which also may limit recruit growth and survival (Dettmers and Stein 1996; Garvey and Stein 1998; Garvey et al. 2002). In the current study, reservoirs containing Gizzard Shad had fewer juvenile Bluegill relative to those that did not contain Gizzard Shad. However, there was no difference in the size of Largemouth Bass recruits among reservoirs with and without Gizzard Shad, suggesting that Gizzard Shad their presence only affected survival, not growth of age-0 bass. Fall abundance of age-0 Largemouth Bass recruits, however, was positively correlated with juvenile Bluegill

abundance in Illinois impoundments with Gizzard Shad. Similarly, Parkos and Wahl (2010) found a positive relationship between Largemouth Bass recruit survival and juvenile Bluegill densities. My findings are consistent with other studies in that Gizzard Shad likely reduced zooplankton densities, indirectly reducing juvenile Bluegill abundance and, therefore, limiting an important prey resource for age-0 bass (Dettmers and Stein 1996; Garvey and Stein 1998; Garvey et al. 2002; Stein et al. 1995). Reservoirs in the current study that contained Gizzard Shad were also more turbid, although turbidity is typically associated with higher productivity and increased zooplankton availability (Bremigan and Stein 2001). Together these findings provide support for the hypothesis that Gizzard Shad deplete prey abundance (i.e., Bluegill) for Largemouth Bass by depleting zooplankton abundance, with indirect negative effects on Largemouth Bass recruit survival (Dettmers and Stein 1996; Garvey and Stein 1998; Garvey et al. 2002).

Reproductive success of Largemouth Bass, as measured by the density of nesting adults, positively affected recruit abundance in study reservoirs containing Gizzard Shad, likely through parental care behaviors that minimize brood loss and/or brood predation (Philipp et al. 1997; Suski et al. 2002; Zuckerman and Suski 2013). This finding indicates that reproductive success, not adult stock abundance, may determine the effect of the adult population on recruit abundance. Similarly, previous work has shown that reproductive success, as measured by peak abundance age-0 bass, was positively correlated with recruit abundance in several Illinois impoundments over multiple years (Parkos and Wahl 2010). Information theoretic modeling in the current study clearly showed that the relationship between reproductive success (i.e., nester density) and recruit abundance was positive, and that, in systems with Gizzard Shad, fish

community dynamics play a more important role in determining Largemouth Bass recruit abundance.

Based on information theoretic model analyses, complex fish community interactions among Bluegill, Gizzard Shad and Largemouth Bass were the most important drivers of Largemouth Bass recruitment in Illinois reservoirs. In reservoirs without Gizzard Shad, other factors failed to significantly predict the abundance of age-0 Largemouth Bass indicating that complex interactions of other variables not included in these analyses were important drivers of Largemouth Bass recruitment. For example, the current study did not include information about the timing of the shift to piscivory in larval bass, which is known to play an important role in growth and survival of age-0 Largemouth Bass (Olson 1996). In addition, the long-term data set used in the current study did not contain zooplankton densities, precluding an in-depth investigation into the exact relationship between Largemouth Bass and zooplankton prey.

There has been reasonable debate regarding the importance of reproductive success and survival of offspring during parental care, relative to first summer predator-prey mechanisms, on the abundance of Largemouth Bass recruits in the fall (Allen et al. 2013; Allen et al. 2011; Parkos et al. 2013; Philipp et al. 1997). The importance of predator prey dynamics during the first summer of life is further supported in the current study, while the role of variation in reproductive success at the level of the population level appears to be less important. Although reproductive success was less important than predator prey dynamics at predicting the abundance of age-0 Largemouth Bass recruits in the fall, there are several factors yet to be studied, and should be the subject of future investigations. To evaluate angling impact, the proportion of nesting bass angled in a population, based on a fisheries-independent estimation of nester density, should be determined. The question still left unanswered is whether angling reduces

reproductive success of a population and, therefore, alters the relative importance of reproductive success in determining recruit abundance.

Lastly, reproductive success may play a more important role in recruitment dynamics across latitudinal and trophic gradients than we observed. For example, higher reproductive success may be more important in recruitment dynamics in northern latitudes where lakes tend to be less turbid, the start of spawning is later in spring, and the window for successful reproduction is short (Kubacki et al. 2002). In more turbid systems in mid- to southern latitudes, prey availability may be a more important determinant of the shift to piscivory, growth, and ultimately survival of age-0 bass than in northern latitudes. Given the diversity of systems in which Largemouth Bass are found. With additional study of the factors that impact population level reproductive success the role that angling nesting bass has on recruitment dynamics can be clarified. Future work utilizing my analytical framework that examines systems from a wider spatial range should provide greater clarity regarding the complex interactions that determine recruit abundance.

CHAPTER 5: SUMMARY AND CONCLUSIONS

The previous chapters have shown how the individual fitness benefits of parental care also have implications for lake-wide recruitment and, therefore, overall population dynamics. I demonstrated at least one way in which predator prey dynamics during the parental care period affects parental care, reproductive success, and ultimately recruitment. That is, in Chapter 2, I found a positive relationship between the rate of consumption of embryos by predators at the earliest stages of development and both brood predator densities plus the duration of exposure of embryos to predation. Management strategies that restrict angling during the spawning season or at least promote rapid release of nesting bass caught by anglers, especially in systems with high densities of brood predators, will minimize the negative impacts of angling on individual reproductive success. In Chapter 3, I demonstrated that when reproductive success was experimentally reduced across all nesting male bass in a population, fall recruit abundance was lower than in a population where reproductive success was not manipulated, but that some level of compensatory survival post-parental care may have partially mediated early mortality losses. The complexity of mechanisms (e.g., reproductive success, shift to piscivory, overwinter survival) dictating survival rates during different stages of the first year of life challenges our ability to identify one single factor or relationship that sets year class strength across a variety of ecological gradients (i.e., differences in latitude, trophic condition). In Chapter 4, I approached this problem by utilizing a set of long-term fish population data spanning over 32 Illinois impoundments and 22 years to evaluate variables hypothesized to affect fall recruit abundance and by applying an information theoretic approach to evaluate which of those variables best predict recruitment in Largemouth Bass. I found that factors related to predator prey dynamics

in the first summer of life (i.e., presence of Gizzard Shad, juvenile Bluegill abundance, turbidity) were the most effective predictors of fall recruit abundance but that reproductive success also plays a role in recruitment dynamics in Largemouth Bass.

I conclude that in addition to well-known mechanisms involving predator prey dynamics during the first summer of life, the results of this dissertation provide support for the hypothesis that reproductive success, and not simple adult stock abundance, has population-level consequences for recruitment dynamics. The results of the pond experiments in Chapter 3 are evidence that reductions in reproductive success result in lower recruit abundance, and model selection tests in Chapter 4 further support the idea that while density dependent survival is important in many populations, variation in nester abundance (and, therefore, reproductive success) in a population indeed coincides with variation in recruitment as well. These results indicate a need to carefully manage angling of nesting Largemouth Bass during the spawning season, at least in systems where fall recruit abundance is sensitive to variations in reproductive success.

Although the advancements gained through the results of this dissertation clarify important aspects regarding Largemouth Bass recruitment dynamics, additional details warrant further investigation. While utilizing long-term data sets provided a powerful tool for examining multiple variables across spatial and temporal scales, the approach lacked the fine-scale resolution needed to better understand the interplay between reproductive success and predator prey interactions during the first summer. For example, estimates of the proportion of males that choose to spawn each year is poorly understood, yet variation in the proportion of spawners likely has important consequences for reproductive success across a population. Reductions in lake-wide reproductive success, therefore, may have varying impact on recruitment dynamics

depending on the proportion of spawners in a given year. Additionally, variations in capture efficiency of anglers, whether due to angler ability or vulnerability of adult bass to capture, would affect the overall impact of angling on reproductive success across a population.

Determining the sensitivity of fall recruit abundance to variations in multiple sources of early mortality during the first year of life can be explored in detail with the development of a robust simulation model that incorporates factors that determine survival rates at multiple stages within the first year of life and then tests how sensitive the response variable (i.e., recruit abundance) is to variation in one or several of predictor variables. Such a simulation model would be necessarily complex, incorporating variability in a large number of parameters that determine mortality rates at each stage of the first year of life. For example, a simulation model should incorporate variation in the proportion of mature adults that choose to mate in a given season, variation in reproductive success due to angling impact (and the several variables that determine angling impact), as well as parameters that capture variation in recruit mortality due to predator prey dynamics in the first summer. Unfortunately, several components of such a simulation model require further investigation to determine the variability and probability distribution of those parameters before the overall simulation model could effectively test the sensitivity of fall recruit abundance to sources of mortality in the first year of life. This approach would build upon the findings of Chapter 4 and would provide greater resolution regarding the question of whether angling is an additive source of mortality during the first year of life.

The presence of Gizzard Shad, juvenile Bluegill abundance, and turbidity were all important predictors of recruitment in model selection analyses reported in Chapter 4, which supports earlier work demonstrating the importance of predator prey dynamics in the first year of life. The pond study I conducted and reported in Chapter 3 was replicated across research ponds

with similar productivity and contained simplified predator prey dynamics because Bluegill and Gizzard Shad were excluded, leaving equal densities of fathead minnows and naturally occurring zooplankton as the only prey resource available to juvenile bass. The results of Chapter 3, therefore, simplified complex interactions that determine survival rates in the first summer and generated results that indicated that survival rates during parental care were indeed important in determining recruitment. One possible implication of the results of these two studies is that the relative importance of sources of mortality at various life stages may vary across trophic or latitudinal gradients. Largemouth Bass are a far-ranging species that inhabit a wide array of aquatic systems, each with a distinct set of abiotic and biotic characteristics. On the broadest scales, environmental and ecological gradients will likely dictate which life stages are critical sources of mortality in the first year of life, while at smaller regional scales, variation in parameters specific to critical life stages will set year-class strength. The model selection study in Chapter 4 provides a framework for assessing recruitment processes at both scales that could be expanded spatially to better address potential differences across the native range of the species.

More broadly, these findings address the need to synthesize an understanding of mechanisms that determine recruit survival at various life stages to identify one or several critical periods of development in the first year of life. It appears that factors important to setting year class strength in Illinois waters may vary across both latitudinal and trophic gradients beyond those studied in this dissertation (i.e., outside Illinois). The findings within this dissertation provide additional clarity on a complex set of mechanisms that determine recruit abundance, but also highlight the need for caution in applying one set of management strategies across the entire species range. In less productive northern systems with shorter spawning seasons, the

importance of reproductive success in determining recruit abundance may be higher than in southern systems that are more productive and have longer spawning seasons, where predator-prey dynamics during the first summer may have a greater impact on recruitment. One important application of this principle may be in the growing interest in tournament angling during the spawning season, and the potential for an intensely negative impact on lake-wide reproductive success in response to such events. In systems were reproductive success has a major role to play in recruitment dynamics, large tournaments held during the spawning season in these systems may be detrimental to recruitment in that year. While populations may be able to withstand such periodic recruitment failures should they occur, making the assumption that negative impacts to reproductive success have little impact on recruitment in all systems would be ill advised. These results as well as earlier work suggest that because of the significant variability among systems, management actions designed to increase reproductive success during the parental care stage to improve recruitment should be considered carefully on a system-by-system basis.

FIGURES AND TABLES

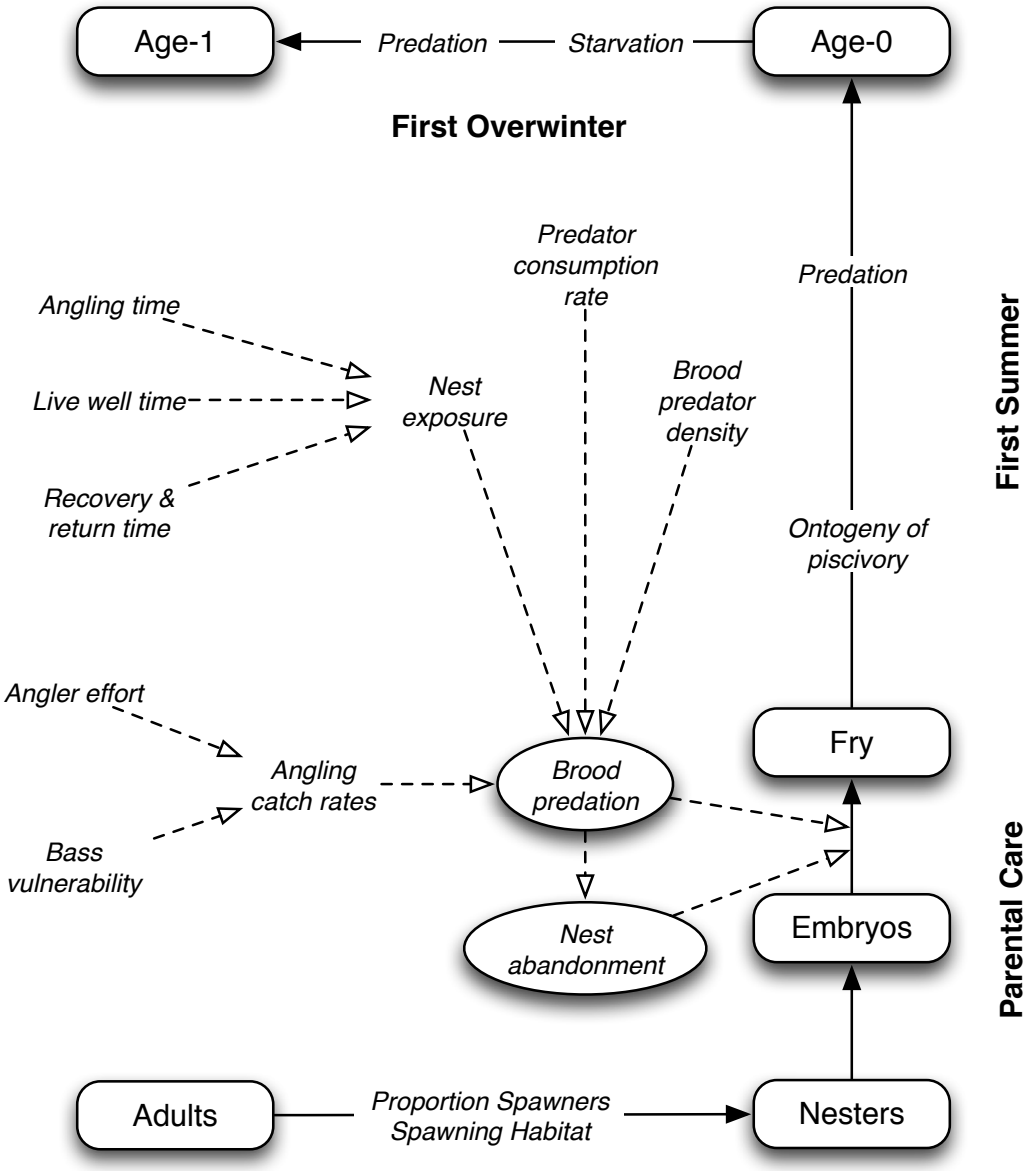

Fig. 1.1. A conceptual model of Largemouth Bass recruitment emphasizing the effect of angling on mortality during parental care. Life stages during the parental care, first summer, and first overwinter phases are in solid rectangles and are connected by solid arrows to represent development from fertilization to age-1 recruits. Factors that affect recruit mortality rates between each stage are in line with the arrows connecting life stages in italics. Brood predation and nest abandonment are in solid ovals and represent sources of mortality related to angling nest guarding male bass. Factors that affect brood predation and nest abandonment (in italics) are connected to ovals by dashed lines.

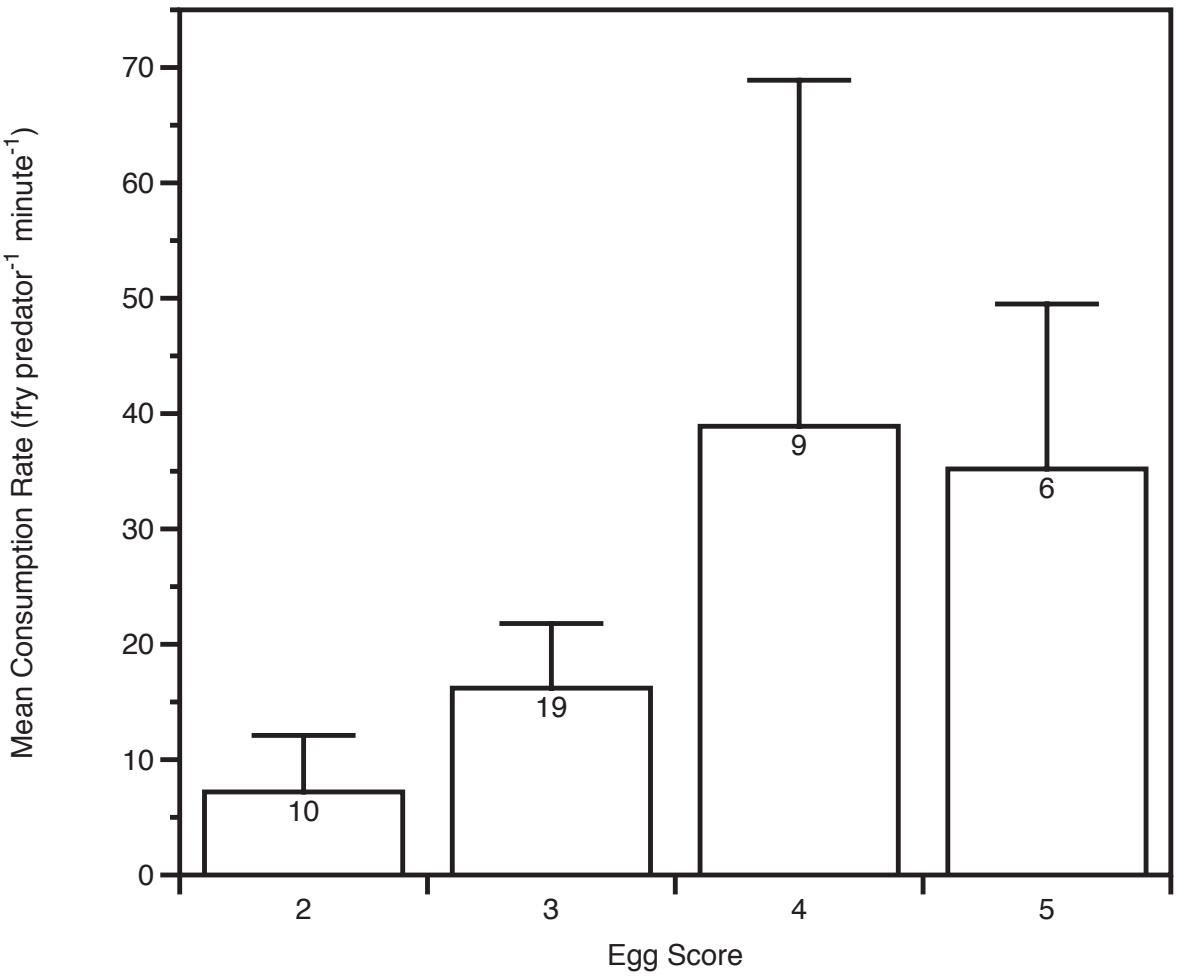

Figure 2.1. Mean consumption rate (fry predator^{-1} minute^{-1}) by egg score. Error bars represent 95% confidence interval on the mean, and numbers indicate number of nests in each egg score group. Post hoc Tukey HSD tests detected no significant pair-wise differences in mean consumption rate. Egg score 1 was not included in the analysis due to low sample size.

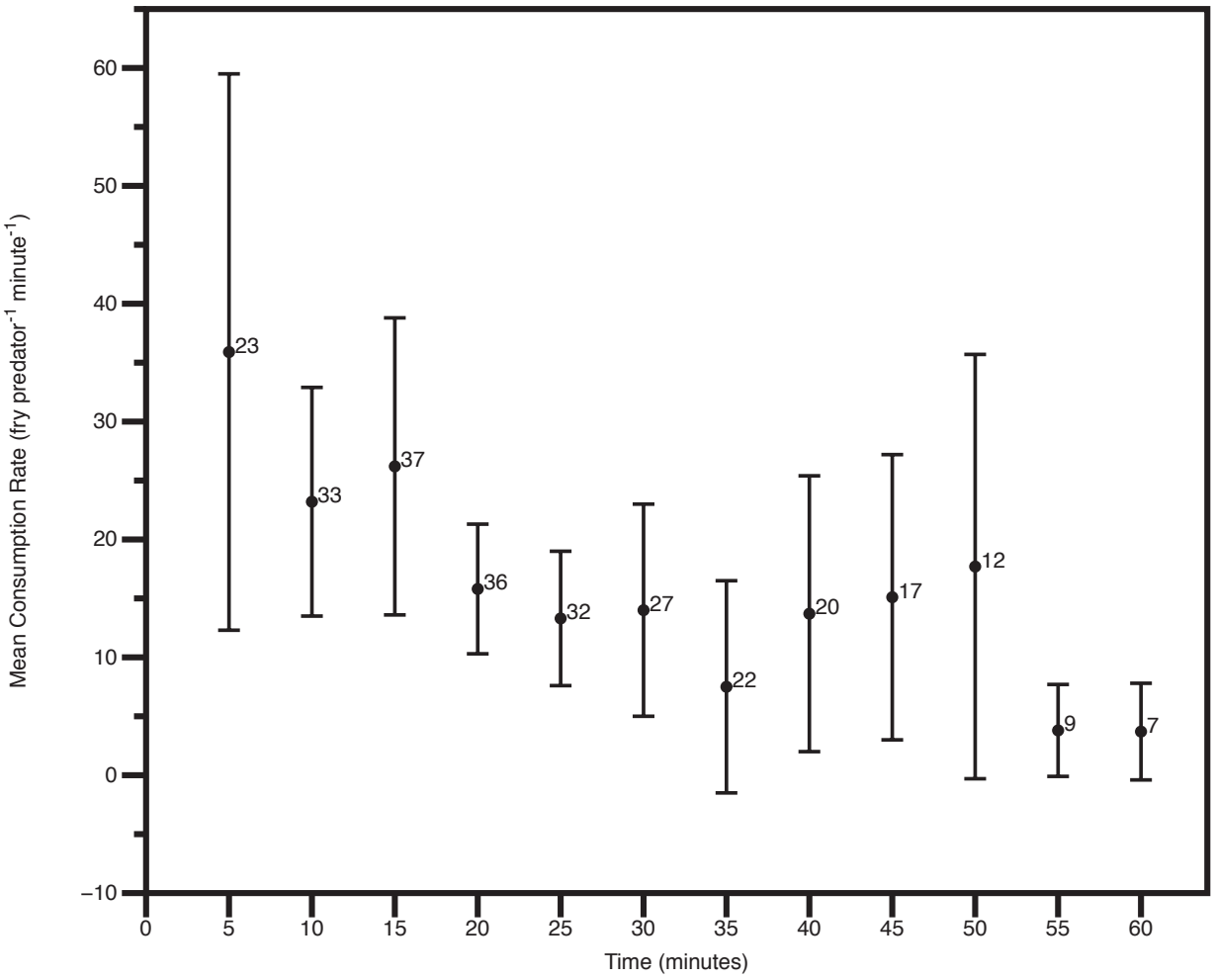

Figure 2.2. Mean consumption rate (fry predator^{-1} minute^{-1}) calculated for all nests on five-minute intervals. Error bars represent 95% confidence intervals on the mean, and labels indicate number of nests included in the calculation of the mean at each time interval.

Table 2.1. Latitude and longitude, number of nests, and mean (standard error) for predator density, male total length (mm), aggression scores, vigilance scores, egg scores (ES) and predation intensity for nine lakes used in the study.

Lake	Latitude Longitude	# Nests	Predator Density	Male TL (mm)	Aggression Score	Vigilance Score	ES	Predation Intensity
Charleston	44° 32’ 04” N 76° 00’ 09” W	3	0.0 (0.0)	418 (44)	0.7 (0.7)	101 (19)	3.0 (0.6)	3.9 (3.9)
Long	44° 31’ 40” N 76° 24’ 09” W	6	0.0 (0.0)	389 (23)	6.5 (2.9)	73 (36)	3.7 (0.3)	2.1 (1.9)
Loughborough	44° 26’ 31” N 76° 25’ 18” W	11	3.2 (1.1)	349 (10)	2.7 (1.2)	114 (14)	3.1 (0.2)	7.4 (2.4)
Maholey	45° 43’ 03” N 74° 48’ 00” W	13	0.6 (0.4)	363 (10)	13.3 (1.8)	145 (10)	3.4 (0.2)	2.5 (1.2)
Mills	45° 47’ 43” N 74° 46’ 54” W	11	9.6 (4.5)	296 (13)	11.4 (2.4)	142 (4)	2.9 (0.4)	8.0 (3.0)
Opinicon	44° 33’ 51” N 76° 19’ 00” W	13	6.4 (1.8)	350 (8)	9.0 (3.5)	126 (6)	3.7 (0.3)	10.8 (2.7)
Otter	45° 48’ 13” N 74° 47’ 41” W	2	0.0 (0.0)	294 (26)	10.0 (3.0)	120 (0)	4.5 (0.5)	6.5 (6.5)
Whitefish	45° 44’ 52” N 74° 49’ 30” W	6	0.0 (0.0)	353 (14)	3.3 (2.3)	127 (5)	3.2 (0.4)	1.9 (1.3)
Wolf	44° 40’ 06” N 76° 28’ 47” W	3	1.3 (1.3)	419 (11)	2.0 (1.0)	100 (22)	3.3 (0.3)	0.2 (0.2)

Table 2.2. Logistic regression evaluating the impact of predator density, male quality, and initial brood size on the likelihood of the occurrence of brood predation across lakes. An asterisk indicates significance at alpha = 0.05.

	Chi-Square	Wald	df	*p*
Full Model	26.551		5	< 0.01*
Predator Density		3.637	1	0.06
Male Quality		6.427	1	0.01 *
Initial Brood Size		4.043	3	0.26

Table 2.3. Cox proportional hazard regression evaluating the timing of the onset of predation after the removal of the parental male relative to predator density, male quality, and initial brood size across lakes. An asterisk indicates significance at alpha = 0.05.

	Chi-Square	Wald	df	*p*
Full Model	30.633		12	< 0.01 *
Lake		16.544	7	< 0.02 *
Predator Density		9.248	1	< 0.01 *
Male Quality		2.478	1	0.12
Initial Brood Size (F_{exp})		6.007	3	0.11

Table 2.4. General linear model evaluating the relationship between predation intensity, male quality and initial brood size on the mean rate of consumption ($\overline{CR}$) of larvae by brood predators across lakes. An asterisk indicates significance at alpha = 0.05.

	df	Mean Square	F-statistic	*p*
Full Model	12	925.33	2.648	0.02*
Lake	7	380.66	1.048	0.42
Predation Intensity	1	535.33	1.474	0.23
Male Quality	1	8.63	0.024	0.88
Initial Brood Size	4	1441.65	6.932	0.14

Table 2.5. General Linear Model evaluating the relationship between the time it took males to return to their nests and predator density, parental male qualities, and initial brood size across lakes. An asterisk indicates significance at alpha = 0.05.

	Chi-Square	Wald	df	*p*
Full Model	22.437		13	0.05*
Lake		17.049	8	0.03*
Male Quality		0.011	1	0.92
Predator Density		0.001	1	0.98
Initial Brood Size		3.966	1	0.88

Table 2.6. Logistic regression evaluating the probability of male abandonment among nests that experience predation relative to male quality, predation intensity and the change brood size due to predation. An asterisk indicates significance at alpha = 0.05.

	Chi-Square	Wald	df	*p*
Full Model	10.612		3	0.01*
Male Quality		4.616	1	0.03*
Predation Intensity		0.788	1	0.94
Brood Size Change		4.149	1	0.04*

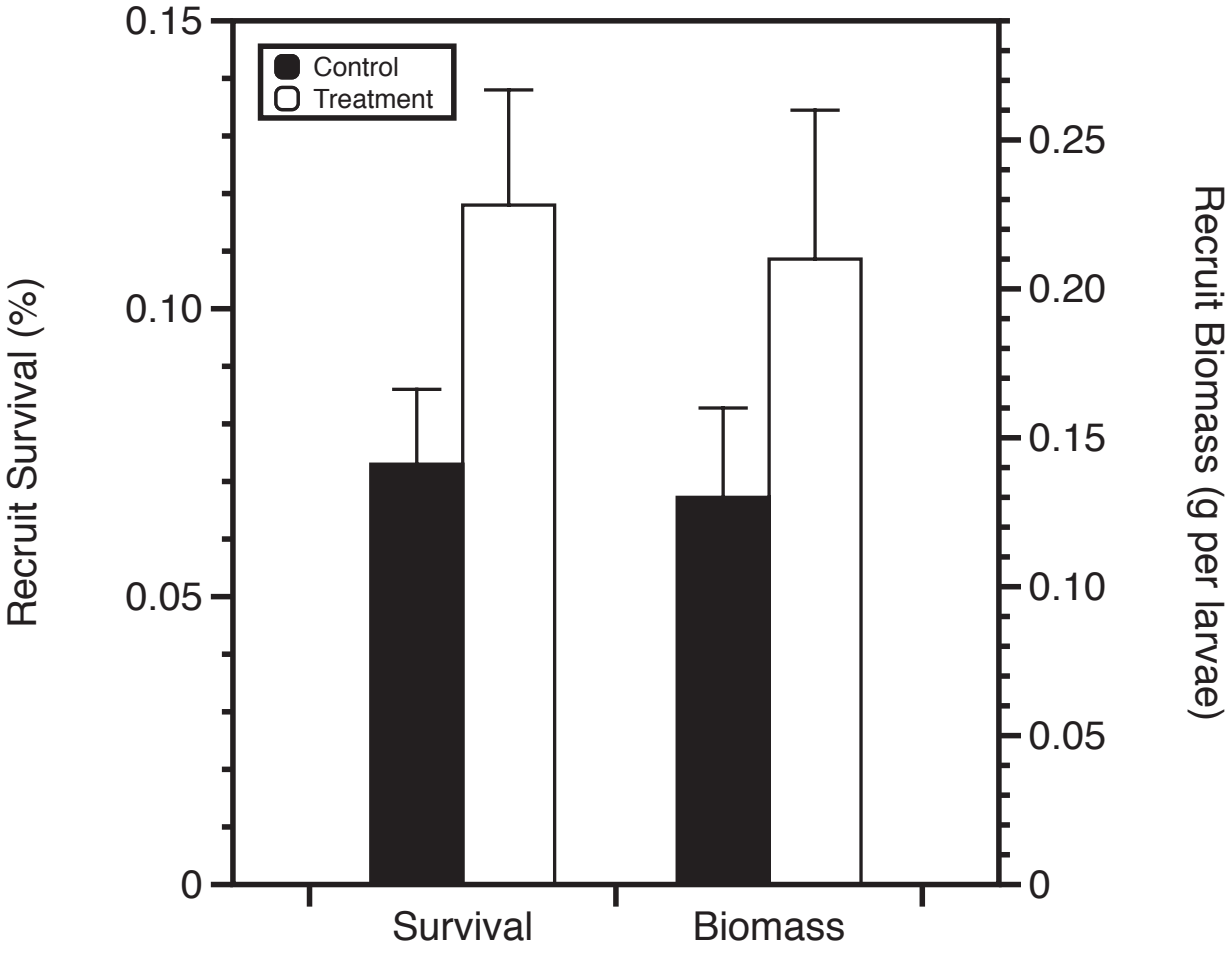

Figure 3.1. Comparison of recruit survival rate and recruit biomass production between treatment (all nests devalued by 50%) and control ponds. Recruit survival rate and biomass production for control (white bars) and treatment (black bars) ponds was calculated as the number and weight (g), respectively, of recruits divided by the estimate of swim-up larvae calculated using the Kubacki conversion. There were no significant differences between treatment and control groups for either measurement.

Table 3.1. Sex, number (n), and mean total length TL (mm) of adult Largemouth Bass used in simulated brood predation experiments in 2007 and 2008, with the number of total nests and successful nests indicated for each pond. Pond numbers followed by a 'T' indicates pond was assigned to the treatment in that year, while pond numbers followed by a 'C' indicate pond was assigned to the control group in that year. Mean TL is followed by the standard error in parentheses.

2007						2008					
Pond	n	TLmm (SE)	# Nests	# Nests Successful	% Nests Successful	Pond	n	TLmm (SE)	# Nests	# Nests Successful	% Nests Successful
3-T	♀ 9 ♂ 11	342 (17) 326 (15)	10	9	90	3-C	♀ 9 ♂ 11	351 (12) 330 (16)	10	9	90
4-C	♀ 10 ♂ 11	338 (19) 324 (15)	7	7	100	4-T	♀ 9 ♂ 11	357 (21) 327 (16)	11	10	91
7-C	♀ 9 ♂ 11	331 (18) 325 (12)	8	8	100	7-T	♀ 9 ♂ 11	343 (15) 336 (13)	8	6	75
8-T	♀ 9 ♂ 11	339 (23) 317 (16)	5	5	100	8-C	♀ 9 ♂ 11	339 (18) 334 (13)	10	6	60
9-C	♀ 8 ♂ 12	308 (20) 317 (10)	8	6	75	9-T	♀ 9 ♂ 11	341 (15) 344 (17)	8	8	100
10-T	♀ 10 ♂ 11	334 (16) 329 (15)	6	6	100	10-C	♀ 9 ♂ 11	355 (18) 331 (16)	6	6	100
11-T	♀ 9 ♂ 11	338 (22) 316 (11)	10	10	100	11-C	♀ 9 ♂ 11	352 (18) 340 (16)	8	7	88
12-C	♀ 8 ♂ 11	332 (15) 325 (13)	7	7	100	12-T	♀ 9 ♂ 11	352 (17) 336 (13)	13	11	87

Table 3.2. Estimate of swim-up larvae, total recruit abundance and biomass (g), recruit survival rates and biomass production, and mean total length (mm) and Fulton's condition factor K for recruits from each pond in 2007 and 2008. Means are reported with standard errors in parentheses.

Year	Pond	Larvae Estimate (n)	Total Recruit Abundance (n)	Total Recruit Biomass (g)	Recruit Survival (%)	Recruit Biomass (g per larvae)	TLmm Mean (SE)	Condition K Mean (SE)
2007	4-C	76950	1843	3165	2.4	0.04	53.3 (0.3)	1.32 (0.01)
2007	7-C	70200	4732	10600	6.7	0.15	52.6 (0.2)	1.32 (0.01)
2007	9-C	64900	5418	7041	8.3	0.10	46.4 (0.4)	1.21 (0.01)
2007	12-C	41520	5945	14934	14.2	0.33	56.1 (0.3)	1.29 (0.01)
2007	**All-C**	**63393 (7696)**	**4485 (915)**	**8935 (2511)**	**7.9 (2.4)**	**0.39 (0.06)**	**52.1 (0.1)**	**1.28 (0.01)**
2007	3-T	18560	2817	10003	15.1	0.53	62.3 (0.3)	1.34 (0.01)
2007	8-T	34725	1501	4357	4.3	0.13	64.0 (0.3)	1.26 (0.01)
2007	10-T	19385	4327	5598	22.0	0.22	42.3 (0.4)	1.27 (0.01)
2007	11-T	28135	3167	6925	11.2	0.24	55.6 (0.3)	1.28 (0.01)
2007	**All-T**	**25201 (3843)**	**2953 (582)**	**6721 (1213)**	**12.7 (3.3)**	**0.54 (0.09)**	**56.1 (0.3)**	**1.29 (0.01)**
2008	3-C	93700	8899	10765	9.5	0.11	43.1 (0.3)	1.42 (0.02)
2008	8-C	53250	4789	5881	8.9	0.10	44.9 (0.4)	1.21 (0.01)
2008	10-C	34220	1567	4424	4.5	0.12	57.9 (0.4)	1.36 (0.01)
2008	11-C	55800	2148	5052	3.7	0.08	54.1 (0.5)	1.24 (0.01)
2008	**All-C**	**59243 (12454)**	**4351 (1670)**	**6530 (1443)**	**6.7 (1.5)**	**0.10 (0.01)**	**47.3 (0.3)**	**1.36 (0.01)**
2008	4-T	44675	4486	6317	9.9	0.12	45.5 (0.5)	1.25 (0.01)
2008	7-T	40750	2806	4572	6.9	0.11	49.1 (0.3)	1.30 (0.01)
2008	9-T	33785	2837	3804	8.2	0.10	43.2 (0.4)	1.38 (0.02)
2008	12-T	25710	4279	6494	16.4	0.22	44.5 (0.3)	1.43 (0.01)
2008	**All-T**	**36230 (4167)**	**3602 (453)**	**5297 (660)**	**10.4 (2.1)**	**0.14 (0.03)**	**47.9 (0.2)**	**1.29 (0.01)**
BOTH - C		**61318 (6822)**	**4418 (882)**	**7733 (1415)**	**7.3 (1.3)**	**0.13 (0.03)**	**56.1 (2.1)**	**1.30 (0.02)**
BOTH - T		**30715 (3351)**	**3278 (363)**	**6009 (694)**	**11.8 (2.0)**	**0.21 (0.05)**	**0.09 (0.02)**	**58.5 (2.0)**

Figure 4.1. Map depicting the location of impoundments included in the study.

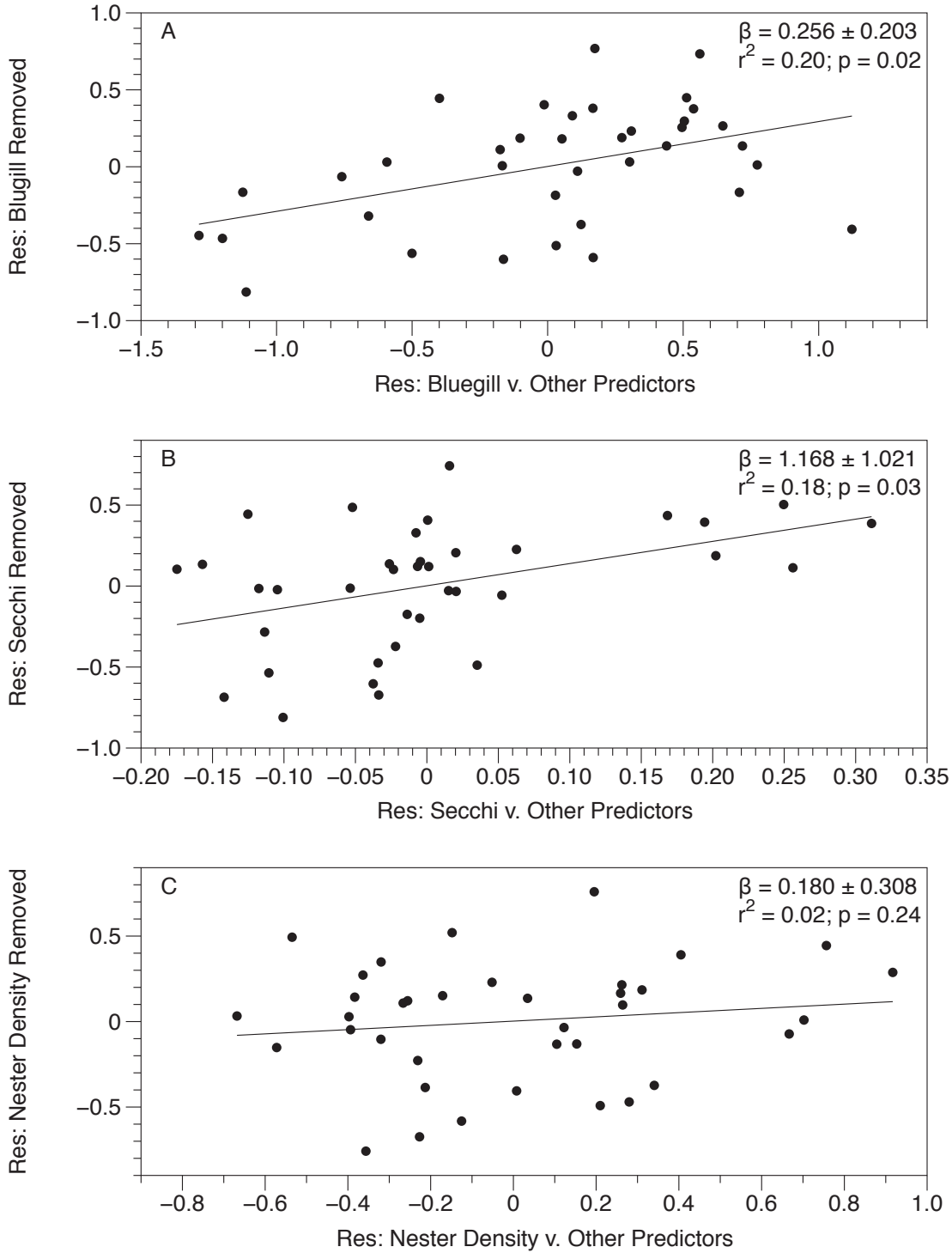

Figure 4.2. Partial regression plots for multiple linear regression model with recruit abundance as the dependent (response) variable nester density (A), juvenile Bluegill abundance (B) and secchi depth (C) as independent predictors. Regression coefficients (β ± 95% confidence limit) and model significance (p) are given.

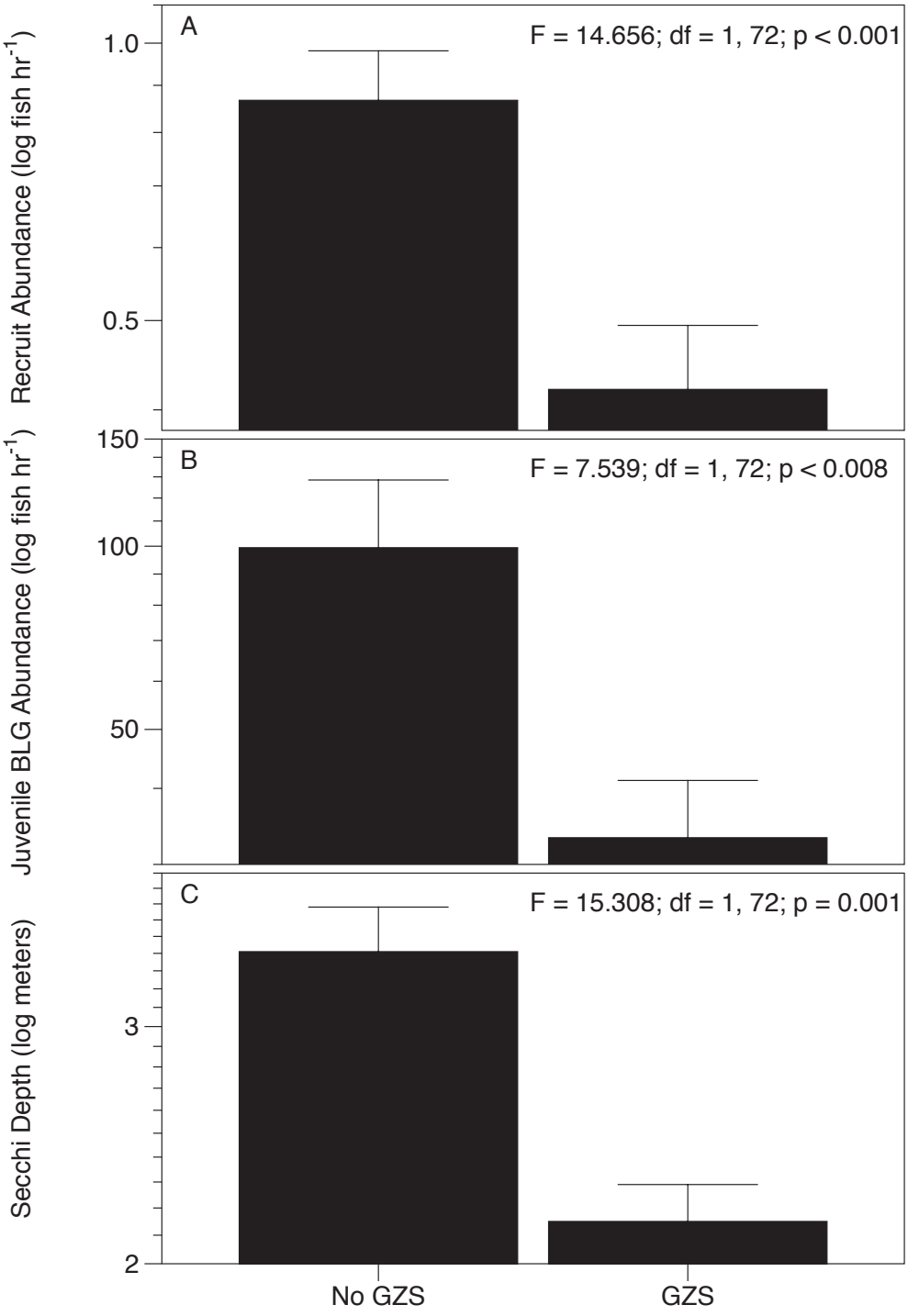

Figure 4.3. Based on GLM model of Gizzard Shad presence, juvenile Bluegill abundance, secchi depth, and nester density, (A) recruit abundance, (B) juvenile Bluegill abundance, and (C) secchi depth was significantly lower in impoundments with Gizzard Shad present. Standard error bars are shown.

Table 4.1. Results of model selection procedures identifying most parsimonious (lowest AICc scores) models predicting Largemouth Bass recruit abundance. Models with AICc < 2.0 are considered highly competitive and models with AICc < 5.0 have less support as predictors of recruitment. Akaike weights (Wc) represent the likelihood that the given model best represents the data. Models with Akaike weights near zero are omitted.

Model	K	SSE	AICc	ΔAICc	Wc
Secchi * GZS Present	4	12.760	-121.49	0.00	0.41
GZS Present	3	13.366	-120.30	1.20	0.22
Secchi * Juvenile BLG * GZS Present	5	11.804	-119.28	2.21	0.14
Nester Density * Secchi * Juv. BLG	6	11.611	-118.09	3.41	0.07
Juvenile BLG * GZS Present	4	12.442	-117.81	3.69	0.06
Secchi * Juvenile BLG	4	12.667	-116.51	4.98	0.03
Secchi	3	14.131	-116.18	5.32	0.03
Max Depth	3	14.368	-114.95	6.55	0.02
Max Depth * Mean Inshore Depth * Secchi * Juvenile BLG * GZS Present	7	9.378	-112.85	8.64	0.01

Table 4.2. Results of model selection procedures identifying most parsimonious (lowest AICc scores) models predicting Largemouth Bass recruit abundance in impoundments containing Gizzard Shad. Models with AICc < 2.0 are considered highly competitive and models with AICc < 5.0 have less support as predictors of recruitment. Akaike weights (Wi) represent the likelihood that the given model best represents the data. Models with Akaike weights near zero are omitted.

Model	K	SSE	AICc	ΔAICc	Wc
Juv. BLG * Secchi	4	4.659	-70.54	0.00	0.65
Juv. BLG * Secchi * Nester Density	5	4.347	-67.30	3.24	0.13
Juv. BLG * Secchi * Nester Density * Release Ratio	6	4.112	-66.49	4.05	0.09
Nester Density * Release Ratio	4	5.338	-65.37	5.17	0.05
Nester Density	3	5.775	-64.89	5.65	0.04
Juvenile Bluegill	3	6.033	-63.23	7.31	0.02
Maximum Depth	3	6.563	-62.82	7.72	0.01
Secchi	3	6.755	-61.69	8.85	0.01

Table 4.3. Correlations of physical habitat of impoundments, characteristics of the parental stock, reproductive success, and first summer growth and survival with abundance of fall age-0 Largemouth Bass recruits. Adjusted r^2 values, F-statistics, degrees of freedom and p-values for each correlation are given. Statistically significant p-values at alpha = 0.05 are indicated in bold.

Model	Adjusted r^2	F-statistic	df	p-value
PHYSICAL HABITAT				
Mean Depth	0.01	1.696	1, 70	0.20
Maximum Depth	0.10	8.634	1, 72	**< 0.01**
Inshore Mean Depth	0.15	12.770	1, 65	**< 0.01**
PARENTAL STOCK				
Adult Abundance	0.02	2.195	1, 56	0.14
Adult Biomass	0.04	3.055	1, 56	0.09
Adult W_r	0.25	19.667	1, 55	**< 0.01**
PSD	0.00	0.491	1, 56	0.49
REPRODUCTIVE SUCCESS				
Nester Density	0.05	4.926	1, 72	**0.03**
Brood Predator Abundance	0.04	3.538	1, 56	0.07
Catch and Release Ratio	0.03	3.286	1,72	0.07
FIRST SUMMER GROWTH AND SURVIVAL				
Degree Growing Days	0.00	0.305	1, 43	0.58
Log Juvenile BLG Abundance	0.09	7.740	1, 70	**< 0.01**
Log Mean Secchi Depth	0.11	9.985	1, 72	**< 0.01**
Gizzard Shad Presence	0.16	14.676	1, 72	**< 0.01**

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